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# **UMI**

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A MONOGRAPHIC REVISION OF  
*SELAGINELLA* P. BEAUV. SUBGENUS *HETEROSTACHYS* BAKER  
IN CENTRAL AND SOUTH AMERICA

by

IVÁN ALBERTO VALDESPINO QUINTERO

A dissertation submitted to the Graduate Faculty in Biology in partial  
fulfillment of the requirements for the degree of Doctor of Philosophy,  
The City University of New York.

1995

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24 February 1995  
Date

Dr. John T. Mickel  
Dr. John T. Mickel  
Chair of Examining Committee  
New York Botanical Garden

2/27/95  
Date

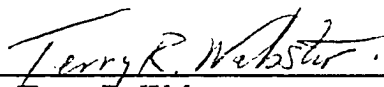
Dr. Richard L. Chappell  
Dr. Richard L. Chappell  
Executive Officer  
Ph.D. Program in Biology  
The City University of New York

William R. Buck  
Dr. William R. Buck  
New York Botanical Garden

Dr. Dennis W. Stevenson  
Dr. Dennis W. Stevenson  
New York Botanical Garden

Thomas E. Jensen  
Dr. Thomas E. Jensen  
Lehman College  
City University of New York

  
Dr. Barbara Meurer-Grimes  
Lehman College  
City University of New York

  
Dr. Terry R. Webster  
University of Connecticut

\_\_\_\_\_  
Dr. Warren H. Wagner Jr.  
University of Michigan

\_\_\_\_\_  
Supervisory Committee

THE CITY UNIVERSITY OF NEW YORK

ABSTRACT

A MONOGRAPHIC REVISION OF

SELAGINELLA P. BEAUV. SUBGENUS HETEROSTACHYS BAKER

IN CENTRAL AND SOUTH AMERICA

by

Iván Alberto Valdespino Quintero

Chairman: Dr. John T. Mickel

A monographic revision of Central and South American species of Selaginella subg. Heterostachys was undertaken, based on comparative gross morphological characters of approximately five thousand herbarium specimens, and on spore morphology as well as on phytochemical studies. As a result of these studies 31 species of Selaginella are classified in subg. Heterostachys in Central and South America. Of these, four are newly described (S. gynostachya, S. hyalogramma, S. karowtipuensis, and S. prolifera), a new variety is proposed within S. sobolifera (S. sobolifera var. arcana), as well as a change of status for S. pearcei (as S. moritziana var. pearcei). The synonymy of the species is fully reviewed and new synonyms are proposed. Selaginella bernoullii is considered a distinct species from S. porphyrospora. In addition, the putative relationships of the species recognized in the area of study are discussed and a key to separate them is also provided.

Of the studied species only S. broadwayi is considered to be a true endemic, whereas the rest of the species with a restricted distribution pattern are expected to be found elsewhere as critical collecting within the area of study is carried out.

Spore morphology study indicates that sculpturing and microstructure patterns of both megaspores and microspores are rather consistent characters within species, and help distinguish species. Spore sculpturing and microstructure patterns are taxonomically useful characters, particularly when more traditional morphological characters fail to clearly separate species.

Study of biflavones in selected species of four of the five subgenera of Selaginella proposed by Jermy (1986, 1990) indicates that the genus is characterized by the presence of robustaflavone, in addition to amentoflavone and hinokiflavone. The biflavonoid patterns of the homophyllous and heterophyllous species within the different subgenera studied were similar. This seems to indicate a close alliance between the homophyllous and heterophyllous selaginellas, perhaps as a result of minor or no changes in the biflavonoid composition of these two groups during the long evolutionary history of the genus. No biflavones were found to help characterize subg. Heterostachys. Additionally, the flavonoid profile of species in series Articulatae was characterized by biflavones rather than by simple flavones as reported by Somers (1978).

Subgenus Heterostachys can be defined by the following syndrome of characteristics: a) lax, flattened, dorsiventral strobili; b) dimorphic sporophylls; c) the largest, dorsal sporophylls laterally spreading, located in the same plane as the

median leaves, with an adaxial laminal flap, and part of the upper (abaxial) epidermis green, composed of polygonal to rounded cells, except for the portion that forms part of the laminal flap, where the epidermis is hyaline to greenish hyaline, composed of elongate and sinuate cells; d) the smaller, ventral sporophylls ascending, located in the same plane as the lateral leaves, without a developed adaxial flap, and with the epidermis of both surfaces frequently hyaline or greenish hyaline, composed of elongate and sinuate cells; and e) axillary or ventro-axillary rhizophores.

## DEDICATION

To my parents, Althea Quintero de Valdespino and Antonio Valdespino,  
for their lifelong support and encouragement that enabled me to pursue and  
achieve this goal.

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To all of them I say: ¡Muchas Gracias!

---

<sup>1</sup> Herbaria acronyms are given according to Holmgren et al. (1988).

## STATEMENT ON NOMENCLATURAL INNOVATIONS

The nomenclatural innovations presented here, including new species, new combinations, change of status, synonymy, etc., indicate the author's intent for future publication. Their inclusion here should not be misconstrued in any case as valid publication under the current rules of the International Code of Botanical Nomenclature.

--The author.

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## CHAPTER I

## INTRODUCTION

"It is therefore necessary from time to time to consult type specimens and re-describe them, as our knowledge of allied species increases."

R. E. Holttum, *Flora of Malaya* (2: 11. 1968)

The genus Selaginella P. Beauv. (the spikemosses), with well over 700 species, is the largest genus of fern-allies and is distributed worldwide, primarily in tropical and subtropical regions (Jermy, 1990; R. Tryon & A. Tryon, 1982). According to Bierhorst (1971), Selaginella "is probably one of the oldest of all extant genera of vascular plants, second only to Lycopodium." The genus probably dates back to the Carboniferous, about 250-300 million years ago (Bierhorst, 1971; Jermy, 1990; Thomas, 1985; Thomas & Quansah, 1991), although some authors suggest a Devonian origin (A. Tryon & Lugardon, 1991). Selaginella appears to be undergoing active speciation (Dixit, 1992; Webster, 1992), and the diversity and extent of asexual reproductive mechanisms in the genus (Kornaś & Jankun, 1983; McAlpin & Lellinger, 1985; R. Tryon, 1955) probably serve to enhance this active speciation, particularly in tropical zones. Although some species are well adapted to dry and exposed areas, in tropical America Selaginella occurs mostly in wet primary forests, and serves as an ecological indicator of environmental conditions (R. Tryon & A. Tryon, 1982).

In an anatomical study of East Indian species of Selaginella, Mukhopadhyay and Sen (1986) concluded that "Selaginella is a mixture of two well defined groups

of elements, and that these two groups evolved from the hypothetical ancestors in two distinct lines of descent." Traditionally, these "two distinct lines" of evolution in Selaginella s.l. (i.e., the homophyllous and heterophyllous species) have been recognized mostly at the subgeneric level (e.g., Braun, 1865; Hieronymus, 1901; Spring, 1849).

Thomas (1992) and Thomas and Quansah (1991) submitted fossil evidence that homophyllous and heterophyllous forms of Selaginella-like plants have been found as distinct groups from the Upper Carboniferous onwards. They concluded that this evidence "provides a clear case for formalizing the taxonomical distinction of at least two genera." Recently, some other authors have suggested the reassessment of the phylogeny and taxonomy of Selaginella (Jermy, 1986; Soják, 1992; Valdespino, 1993a).

Few characters (i.e., monomorphic stem leaves and lack of axillary leaves) support the homophyllous group. The species alliances within this group could be recognized at the subgeneric level as in Jermy's (1986, 1990) classification system (i.e., subg. Selaginella, subg. Ericetorum Jermy, and subg. Tetragonostachys Jermy), or at the generic level as recently done by Soják (1992), who described a segregate genus, Bryodesma, which corresponds to subg. Tetragonostachys.

The group formed by the heterophyllous selaginellas according to Jermy's system (i.e., subg. Stachygynandrum (P. Beauv.) Baker, including series Articulatae Spring and subg. Heterostachys Baker) seems to be supported by a number of characters (e.g., presence of axillary leaves, leaf dimorphism, and rhizophores, the

latter being ventral or axillary, except mostly in series Articulatae of subg. Stachygynandrum, where they are dorsal). However, homophyllous species classified within subg. Tetragonostachys (= Bryodesma) also possess rhizophores, but in a dorsal position. Therefore, it is not clear yet whether the characters shared by these two groups evolved by parallelism, whether they represent reversals to an ancestral condition, or whether they are synapomorphies that may indicate a closer relationship between them than currently thought.

A continuing obstacle we face in trying to elucidate problems of relationships in the genus Selaginella is our poor knowledge of the groups concerned. At the present time only the homophyllous subg. Tetragonostachys (Tryon, 1955) and species in the S. sulcata group s.str. series Articulatae of subg. Stachygynandrum (Somers, 1978) have been monographed in a geographically inclusive manner. Most modern treatments of Selaginella have been floristic in essence, e.g., Bizzarri (1975: Ethiopia), Dixit (1992: India), Fraile et al. (in press: Central America and the southernmost part of Mexico), Mickel and Beitel (1988: Oaxaca, Mexico), Smith (1981: Chiapas, Mexico), Stolze (1983: Guatemala), Tagawa and Iwatsuki (1979: Thailand), Valdespino (1993a: North America), Wong (1982: Malaysia), or taxonomic revisions focused on a specific region e.g., Dahlen (1988: Hong Kong), Quansah (1986: West Africa and Madagascar).

In this context it is proper to mention the work of one of the most influential figures in the study of Selaginella during this century, A. H. G. Alston. Alston, based at the British Museum of Natural History, London, became an

established specialist of Selaginella during the first part of this century. He published numerous floristic accounts that have been summarized by Jermy (1990). Those dealing with the New World include Trinidad and Tobago (1934a), Brazil (1936), Surinam (1938), Argentina, Uruguay, and Paraguay (1939); West Indies (1952), Continental North America (1955), and South America (1981, published with Jermy and Rankin). One of his achievements was to solve, to a certain extent, many nomenclatural problems that plagued Selaginella. These problems were the result of decades in which the taxonomy of the genus was dominated by very narrow species concepts, misconception of species caused by the lack of study of type material, and the carelessness of some workers. Although his treatments provide keys, synonymy, distribution data, and specimen citations with occasional discussion, he provided no species descriptions except for new species. Moreover, there is hardly any indication of his concepts on species relationships (Jermy & Rankin, in Alston et al., 1981; Somers, 1978; Valdespino, 1992), except in the last treatment published before he died (Alston, 1955) and in the one published posthumously in 1981. In those treatments, species in series Articulatae were kept together in the key and in the conspectus of the taxa. He, however, did advance a classification (Walton & Alston, 1938) that corresponded almost entirely to that proposed by Baker (1883, 1887) (see Alston et al., 1981 and Somers, 1978, for additional comments), but that was ignored for the most part in his treatments. This, in part, has contributed to the lamentable practice by some contemporary authors of neglecting placement of newly published species or the ones treated in

floristic accounts within any previous classification system, thus making the genus more enigmatic to nonspecialists. As a result, and together with the mostly microscopic nature of the characters found in Selaginella, it has become difficult for modern botanists to understand this genus, to be able to recognize species, and to assess and develop concepts on species group relationships (Dahlen, 1988). Nevertheless, the reputation of Selaginella as being a relatively difficult genus taxonomically (Dahlen, 1988) is to a certain degree unjustified. As pointed out by Buck (1986), it has to do more with a certain reluctance by researchers to look at the distinguishing characters of the species with proper magnification (i.e., a good dissecting microscope and a compound microscope), rather than to the complexity of the genus itself. This is particularly distressing since early last century Greville and Hooker (1831) had already complained that the genus Lycopodium (in the broadest sense as to include Selaginella) had been studied "without, in short, the same careful and microscopic investigation that is required for studying the mosses."

While conducting field work in Panama with Dr. Dennis Stevenson of The New York Botanical Garden, a group of small selaginellas, living on the forest floor under shaded and humid conditions (Fig. 1) intrigued me because of their bluish green, iridescent leaves. The initial enthusiasm for these Panamanian selaginellas prompted me to search through the Pteridophyte Herbarium of The New York Botanical Garden in order to identify them and to look for other species with similar characteristics. After much searching it became clear to me



that, as aforementioned, identification of species and species groups with the existing literature was a nearly hopeless task. Finally, upon careful examination of their characteristics and comparison with specimens previously determined I was able to identify them and concluded they belonged to subg. Heterostachys.

In the Neotropics, there are about 250 species of Selaginella, mostly classified in the heterophyllous subgenera Stachygynandrum and Heterostachys. Subgenus Stachygynandrum possesses approximately three-fourths of the total number of species. Subgenus Heterostachys, on the other hand, is comprised of some 40 species, of which about 31 species including 5 varieties are found in Central and South America (see Appendix IV). I estimate that in total there are some 150 species of this subgenus worldwide. On the other hand, Jermy (1990) estimated only about 60 species worldwide.

Subgenus Heterostachys as defined by Baker (1883, 1887) is characterized by having "ordinary leaves of two kinds, and spreading in two planes. Bracts [sporophylls] also of two kinds, but the spikes resupinate (i.e., the smaller bracts in the same plane as the larger leaves, and vice versa)."

I decided that since at that time there were no other New World botanists working on Selaginella, I would familiarize myself with it, particularly with the species in subg. Heterostachys. I began my studies by trying to find a set of characters that will more fully define this subgenus.

The subg. Heterostachys as defined here is characterized by the following syndrome of characters: a) lax, flattened, dorsiventral strobili; b) dimorphic

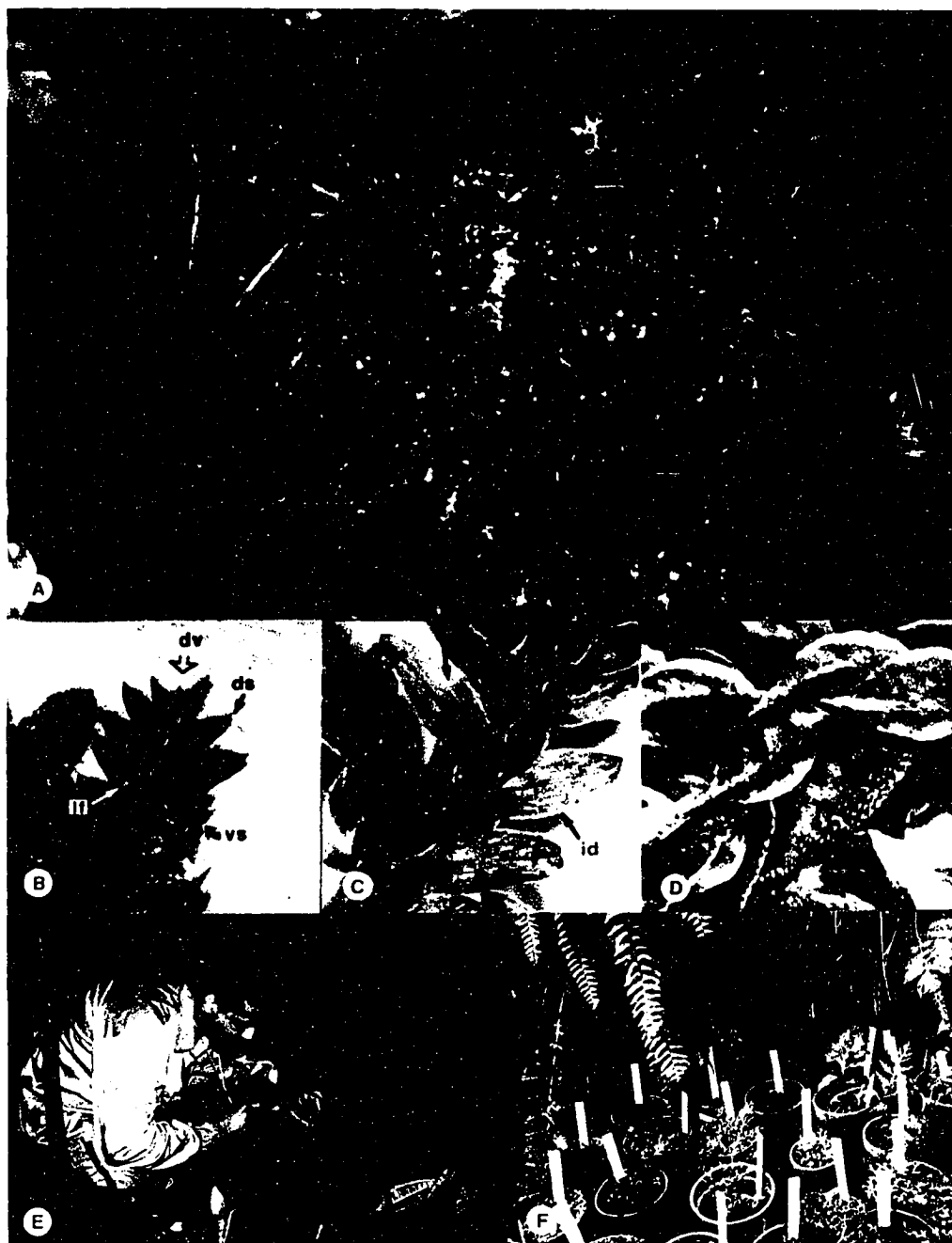
sporophylls; c) the largest dorsal sporophylls located in the same plane as the median leaves, laterally spreading, with part of the lower (adaxial) epidermis fused to form a laminal flap (see Goebel, 1905; Mukhopadhyay & Sen, 1981; Quansah & Thomas, 1985), and part of the upper (abaxial) epidermis green, composed of polygonal to rounded cells, except for the portion that forms part of the laminal flap, where the epidermis is hyaline to greenish hyaline, composed of elongate and sinuate cells; d) the smaller ventral sporophylls located in the same plane as the lateral leaves, ascending, without a developed adaxial flap, and with the epidermis of both surfaces frequently hyaline or greenish hyaline, composed of elongate and sinuate cells; and e) axillary or ventro-axillary rhizophores. In addition to these characteristics, many species of subg. Heterostachys have bluish green, iridescent leaves, many have idioblasts on one or both surfaces of either the median leaves, lateral leaves, and sporophylls, or in all or two of them, and some possess short or long hairs on the upper surface of the lateral leaves (Jermy, 1985; Valdespino, 1993b), frequently near the basiscopic margin or infrequently throughout the upper surface (see Figs. 1-4).

In the present monographic study, the West Indian species of Selaginella subg. Heterostachys (ca. 9 species) have been excluded because, with the exception of S. armata Baker, S. eatonii Hieronymus ex Small, and S. tenella (P. Beauv.) Spring, they are endemic to this area and/or seem to form a natural alliance distinct from the mainland species. Most of these species, which provisionally include S. armata, S. cordifolia (Desvaux ex Poiret) Spring, S. eatonii, S. laxifolia

Baker, S. plumieri Hieronymus, S. tenella (syn. S. subcaulescens Baker), S. wilsonii Hieronymus, and two undescribed taxa, will be dealt with fully in the Selaginella treatment for the Flora of the Greater Antilles Project. It is expected that as part of this project field work will be conducted in that region, fresh material for laboratory studies will be collected, and thus a better understanding of the West Indian species of subg. Heterostachys will be obtained.

Figure 1. Habit, characteristics, collection, and propagation of species of subg.

Heterostachys in Central and South America. A. Habit of Selaginella moritziana (Valdespino et al. 1327, NY). B & D. Selaginella popayanensis (Alston 7906, NY,). B. Lower surface view of the dorsiventral strobilus (dv); note laminal flap (lf), ventral sporophylls (vs), and dorsal sporophylls (ds) (30×). D. Detail of upper surface of the lateral- and median leaves; note arrows indicating short hairs (h) near the basiscopic margin of the lateral leaves (40×). C. Selaginella tenella (Valdespino 1367, NY) (40 ×). C. Detail of the upper surface of the lateral- and median leaves; note arrows indicating leaf idioblasts (id). E. Collection of Selaginella specimens in the cloud forest of Fortuna region, Panama. F. Selaginella species collected in the wild and now propagated at the New York Botanical Garden Propagation Center.



## CHAPTER II

### TAXONOMIC HISTORY AND CLASSIFICATION OF *SELAGINELLA*

#### II.1. TAXONOMIC HISTORY OF *SELAGINELLA*

Species of the genus Selaginella, including the native S. denticulata (L.) Spring, S. helvetica (L.) Spring, and S. selaginoides (L.) P. Beauv. ex Schrank & Martius, were long known to European naturalists. Initially, these and other species were given polynomial names and often included in the genus Muscus (see Dillenius, 1741) or under polynomic generic names (e.g., Breyne, 1678; Ray, 1693).

The earliest formal account of what is now called Selaginella is found in Dillenius (1741), who described two genera: Selaginoides with only one species (= S. selaginoides) and Lycopodioides, a genus including eleven taxa of heterophyllous selaginellas and two other species, one each currently assigned to Lycopodium and Psilotum. Dillenius' genera were combined by Linnaeus (1753) within his very broadly defined genus Lycopodium. The generic names Selaginoides and Lycopodioides were later validated by Séguier (1754) and Boehmer (1760), respectively. However, species of Selaginella continued to be described as Lycopodium (e.g., by Lamarck, 1791) until Palisot de Beauvois (ex Mirbel in Lamarck & Mirbel, 1802) and Palisot de Beauvois (1805a) segregated the spikemoss genus Stachygynandrum from Lycopodium. In other publications, Palisot de Beauvois (1804, 1805b) recognized four genera: Selaginella (= Selaginoides sensu Dillenius and Séguier), Diplostachyum, Gymnogynum, and

Stachygynandrum (the last three genera composed nearly entirely of heterophyllous selaginellas and corresponding essentially to Lycopodioides sensu Dillenius and Boehmer). Regretfully, most of Beauvois' contemporaries (e.g., Poiret, 1814; Desvaux 1827; Gaudichaud, 1828; Greville & Hooker, 1831; Raddi, 1825) disregarded his genera and continued to describe species in Lycopodium.

A. F. Spring, in a series of papers (1838, 1839, 1840, 1843, 1846) and in the only major monograph of the genus Selaginella (1849), combined all Palisot de Beauvois' genera into a very broadly defined Selaginella. Spring (1846) summarized the reasons to reject Palisot de Beauvois' generic concepts as follows: 1) the name Stachygynandrum denoted "une chose qu'on ne peut démontrer chez les Lycopodiacees, une différence sexuelle" (the existence of sexuality in Lycopodiaceae, which according to him could not be proved); and 2) that Palisot de Beauvois (1805b) himself had abandoned an early definition (P. Beauvois, 1805a) of the genus Stachygynandrum and divided it into four genera: Selaginella, Gymnogynum, Diplostachyum, and Stachygynandrum. Therefore, he thought it better to adopt Selaginella, as delimited by A. Braun (apparently in an unpublished manuscript) in order to avoid new confusion in the synonymy of both genera and species. His judgment usually has been followed ever since. Nonetheless, Spring (1846: 326-327) did recognize that there were some species, S. rupestris (L.) Spring, S. selaginoides, S. bryoides (Kaulf.) Spring [= S. pygmaea (Kaulf.) Alston], S. sanguinolenta (L.) Spring, that ought to be separated from Selaginella. And, of course, we now know that sexuality does indeed exist in

Selaginella. Thus, some later authors (Kung, 1988; Kuntze, 1891; Rothmaler, 1944) have segregated other genera based on the original generic concepts established by Dillenius and Palisot de Beauvois, or on other grounds (Soják, 1992). A more detailed historical account is found in Pichi-Sermolli (1971), Thomas and Quansah (1991), and Soják (1992).

## II.2. CLASSIFICATION SYSTEMS OF *SELAGINELLA*

Previous work on the taxonomy and phylogeny of Selaginella s.l. (e.g., Alston, 1955; Alston et al., 1981; Baker, 1883, 1887; Braun, 1865; Dahlen, 1988; Hieronymus, 1901; Jermy, 1986, 1990; Spring, 1849; R. Tryon, 1955; Walton & Alston, 1938; van Alderwerelt van Rosenburgh, 1911, 1915; Warburg, 1900) have been based on morphological characters such as strobilus symmetry, arrangement and morphology of vegetative and fertile leaves, stelar patterns, and plant habit (Thomas & Quansah, 1991; Soják, 1992). The classification schemes are summarized in Table I.

It should be noted that most of these classification systems are essentially similar to and to a certain degree only elaborations of Spring's system (1849) (see Table I). They all recognize basically two major groups, homophyllous and heterophyllous selaginellas. Moreover, differences are mainly found at the taxonomic level in which one group is recognized or further subdivided. Hieronymus' system is somewhat different from the others in that he introduced morphology of spores and distribution of sporangia within the strobili, as well as



the number of steles, as useful taxonomic characters.

Previous to these classifications, Greville and Hooker (1831) had recognized a group of species within Lycopodium s.l. (including Selaginella) characterized by "Spicis compressis unilateralibus, squamis inaequalibus" (flattened, dorsiventral strobili, and dimorphic sporophylls), which they referred to as the Platystachya group. Spring (1843, 1846, 1849) was the first to formally recognize this group in Selaginella in his "amentis unilateralibus, bracteis dimorphis" (dorsiventral strobili and dimorphic sporophylls) Platystachyae group. He further subdivided this group by whether or not the strobilus was resupinate (a condition resulting from a 180° rotation of the fertile axis according to Jermy et al. (1967), and Jermy (1985), but see discussion in Morphology section), consequently the largest dorsal sporophylls are in the same plane as the median leaves and the smaller ventral sporophylls are located in the same plane as the lateral leaves). In most of the other classifications (see taxa with dotted background in Table I), species with resupinate, flattened, dorsiventral strobili, and dimorphic sporophylls (Figs. 1B; 4), were also recognized as a natural group, often at the subgeneric (as subg. Heterostachys: Baker, 1883, 1887; Warburg, 1900; Walton & Alston, 1938; Jermy, 1986, 1990) or at the subsection or series (Braun, 1860, 1865; Hieronymus, 1901; van Alderwerelt van Rosenburgh, 1911, 1915) ranks.

The most recent classification of Selaginella s.l. (Jermy, 1986, 1990), a modification of Baker's system, divides it into five subgenera. This system differs from others in that it divides the homophyllous selaginellas into three subgenera:

subg. Selaginella, subg. Tetragonostachys, and subg. Ericetorum. The heterophyllous selaginellas are divided into two subgenera: subg. Stachygynandrum, in which subg. Homostachys Baker is included, and subg. Heterostachys, which is narrowly defined with only 60 species worldwide.

The species of subg. Heterostachys share several characters with subg. Stachygynandrum and subg. Homostachys of Baker. However, it is not clear whether these groups should be recognized as sections or subgenera.

The recent recognition of a segregate genus, Bryodesma, from Selaginella by Soják (1992) prompts a reevaluation of the concept of one inclusive and heterogeneous genus, Selaginella, vs. the assemblage, at the generic level, of two or possibly four discrete and homogeneous groups (i.e., Bryodesma, Selaginella, and two unnamed genera). The recognition of two or more genera within Selaginella would have a profound nomenclatural impact. The generic name Selaginella is nomenclaturally attached to only two species (S. selaginoides and S. deflexa Brackenridge). New combinations would, thus, have to be made for ca. 400 species that do not have available names. This problem has probably deterred most active workers on the genus from recognizing several genera within Selaginella. It may be possible, however, to retain the generic name Selaginella for the larger heterophyllous alliance of species by proposing the conservation of the name with a different type, as permitted by the current International Code of Botanical Nomenclature (Greuter, 1994). This task falls outside the scope of my present study but remains a project to be developed in the near future.

Table I  
CLASSIFICATION SCHEMES FOR THE GENUS *SELAGINELLA*

| Spring (1849)                 | Braun (1865) <sup>2</sup>          | Baker (1883, 1887)        | Warburg (1900)             |
|-------------------------------|------------------------------------|---------------------------|----------------------------|
| Sect. I. Homoeophyllae        | A. Homotropae                      | Subg. I. Selaginella      | Subg. I. Euselaginella     |
| Sect. II. Heterophyllae       | a. Polystichae                     | Subg. II. Stachygynandrum | Subg. II. Boreoselaginella |
| 1. Tetragonostachyae          | α. Cylindrostachyae                | Series:                   | Series:                    |
| A. Circinatae                 | β. Tetragonostachyae               | 1. Decumbentes            | 1. Rosulatae               |
| B. Complanatae                | b. Tetrastichae                    | 2. Ascendentes            | 2. Decumbentes             |
| a. Continuae                  | B. Dichotomae                      | 3. Rosulatae              | 3. Radicantes              |
| b. Articulatae                | a. Continuae                       | 4. Sarmentosae            | 4. Ascendentes             |
| 2. Platystachyae <sup>1</sup> | α. Tetragonostachyae               | 5. Scandentes             | Subg. IV. Homostachys      |
|                               | β. Platystichae                    | 6. Cauliscentes           | Subg. V. Heterostachys     |
|                               | b. Articulatae                     | Subg. III. Homostachys    |                            |
|                               |                                    | Subg. IV. Heterostachys   |                            |
| Hieronimus (1901)             | v.A.v.R. (1911, 1915) <sup>4</sup> | Walton & Alston (1938)    | Jermy (1986, 1990)         |
| Subg. I. Homoeophyllum        | A. Heterophyllum                   | Subg. I. Euselaginella    | Subgenera:                 |
| Sect.:                        | 1. Monostelicae                    | Subg. II. Stachygynandrum | I. Selaginella             |
| 1. Cylindrostachyae           | a. Homoeostachys                   | Series:                   | II. Ericetorum             |
| 2. Tetragonostachyae          | b. Heterostachys                   | 1. Decumbentes            | III. Tetragonostachys      |
| Subg. II. Heterophyllum       | 2. Pleiostelicae                   | 2. Ascendentes            | IV. Stachygynandrum        |
| Sect.:                        | a. Sarmentosae                     | 3. Sarmentosa             | V. Heterostachys           |
| 1. Pleiomacrosporangiatæ      | b. Cornosae                        | 4. (Omitted)              |                            |
| Series:                       | B. Isophyllum                      | 5. Cauliscentes           |                            |
| A. Monostelicae <sup>3</sup>  | C. Homoeophyllum                   | 6. Circinatae             |                            |
| B. Pleiostelicae              |                                    | 7. Articulatae            |                            |
| 2. Oligomacrosporangiatæ      |                                    | Subg. III. Homostachys    |                            |
| Series:                       |                                    | Subg. IV. Heterostachys   |                            |
| A. Continuae                  |                                    |                           |                            |
| B. Articulatae                |                                    |                           |                            |

Table I (continued)

1. Dotted background denotes the relative placement of species of subg. Heterostachys, as defined here, on the different classification schemes proposed.
2. Braun (1860) proposed a similar classification system. This system, with minor modifications, is essentially the same presented here (Braun, 1865).
3. Partial dotting denotes the scattered placement of species here recognized under subg. Heterostachys within different species groups of series Monostelicae.
4. v.A.v.R., corresponds to van Alderwerelt van Rosenburgh.

## CHAPTER III

### MORPHOLOGY

#### III.1. LEAF MORPHOLOGY

Leaf morphology is one of the most important sources of characters to distinguish the species of Selaginella. This criterion has been extensively used in all treatments of the genus (Dahlen, 1988; Somers, 1978). The shape, width, and length of the leaf, the presence and position of marginal projections (e.g., teeth, cilia), the shape of the leaf apex (e.g., acute, acuminate, obtuse), the shape of the leaf base (e.g., rounded, oblique, auricled), are some of the characteristics commonly used to separate species (e.g., Buck & Lucansky, 1976; Dahlen, 1988).

In this monograph, I have made extensive use of some additional characters such as length of the apices, vestiture of the leaf (i.e., whether the species have hairs throughout the upper surface of the leaf or whether the hairs are restricted to the basiscopic margin), the presence of idioblasts on the surfaces of the leaves and sporophylls, the distribution of stomata on the surfaces of the leaf, and cellular characteristics of the margin (e.g., whether it is formed by hyaline or greenish, elongate cells, whether it has marginal stomata or not). Although Jermy (1990) considered that leaf shape was best observed on leaves located on the basal part of secondary branches, I have found, on the contrary, that leaf shape is best observed on leaves located along the central portion of the main stem. As similarly pointed out by Somers (1978), assessment of leaf shape and size made

on leaves taken from branches, from along the most apical and basal portion of the stem, and from the central portion of the stem, vary greatly. Accordingly, shape and size were recorded from leaves taken from the main stem, primarily from the central part of it. The measurements were not used, however, as the principal character to separate species. Dahlen (1988), examining leaves of Hong Kong species of Selaginella, found that although the means of leaf size differ significantly between species, the absolute ranges overlapped. I consider the use of leaf size as an unreliable character, especially when it is used as the only diagnostic feature. A similar conclusion was reached by Somers (1978) working with the S. sulcata group of series Articulatae. Instead, I have used proportional ratios of the leaf, which were found to be a more constant character, but again were employed to a minimal degree and in combination with other characters. This was used, in particular, when contrasting the length of the apex (e.g., acumen, arista) relative to the length of the leaf lamina. In general, I have relied more on qualitative characters (e.g., leaf idioblasts, marginal projections, presence of hairs on the surfaces of the leaf, leaf shape), which seem to be more constant among and within taxa.

### III.2. EPIDERMAL CELL PATTERNS

In most heterophyllous species of Selaginella, the adaxial surface of the lateral and median leaves, as well as the abaxial surface of both leaves have different epidermal patterns (Harvey-Gibson, 1897; Satake, 1934; Mital, 1969). In

the heterophyllous series Articulatae, however, this variation is found in only one species (Somers, 1978). In the Articulate series, both surfaces of the leaf are composed of elongated cells.

Although morphologically precise, the terms "adaxial" and "abaxial" may be rather confusing. In Selaginella the upper surface of the lateral leaves corresponds to the adaxial surface, and on the median leaves corresponds to the abaxial surface. Conversely, the lower surface of the lateral leaves is abaxial and the lower surface of the median leaves is adaxial. Contrary to what may be expected, the epidermal pattern of the adaxial surface of the lateral leaves does not correspond to that of the median leaves and similarly the abaxial surface of the lateral leaves does not correspond to that of the median leaves. This terminology sometimes becomes cumbersome and does not help the nonspecialist to understand species descriptions. Accordingly, I have decided to follow closely Mital (1969) and refer to the surfaces of the leaves only as "upper" and "lower" surfaces. Alternatively, these two surfaces could have been referred to, for more precision, as "ligular" (= adaxial) or "aligular" (= abaxial) surfaces as done by Harvey-Gibson (1897). I am reluctant to the use of these terms, however, because less experienced students would have to determine first where the ligule is located in each leaf, which may be time-consuming and sometimes difficult to determine, before observing and evaluating the epidermal patterns of the leaf itself.

In surface view under the light microscope (LM), the upper surface of the median and lateral leaves, and part of the upper surface of the dorsal sporophylls

(at least in neotropical species of subg. Heterostachys), are generally composed of polygonal cells that appear isodiametric or rounded (Figs. 2A-E; 3E-G). The outline varies considerably from sinuous to almost straight. Similar findings were reported by Dahlen (1988), who attributed them to variations between the outer and the inner portions of the cell wall. Under scanning electron microscope (SEM) view, these cells appear rounded and globose with a concave to somewhat sinuate outline (see Figs. 2F & G; 3A-E). Dahlen (1988), using SEM, reported these cells to be convex in outline. The lower surface of the median and lateral leaves of the dorsal sporophylls, and of both surfaces of the ventral sporophylls, are generally composed of elongate cells with sinuate outlines, that have pointed to truncate apices. They appear more or less rectangular in surface view with both the LM and SEM. Additionally, under SEM, these cells also appear more globose (Figs. 2H; 3F-H).

Both types of cells (polygonal and elongated) have projections here referred to, following Somers (1978), as "papillae" (see Figs. 2B & F; 3A-G). Other authors refer to these projections as "verrucae" [verrucae] (Bienfait & Waterkeyn, 1974), "warts" (Dahlen, 1988), or "warty thickening" (Mukhopadhyay & Sen, 1986). There are usually many of these papillae per cell (Figs. 3A-G), but there may be as few as one (Fig. 2B). Additionally, SEM view of the upper surface of the leaves shows some minor projections that resemble small granules (Figs. 3B-D) that presumably are smaller cuticular projections.

In some species, there are modified, elongated cells on the upper surface



of lateral and median leaves, dorsal sporophylls, on the lower surface of the lateral leaves and ventral sporophylls, and frequently along the margins (Figs. 2B; 3B). These types of cells are often referred to as "cuticular flaps" (Jermy, 1985), "sclerotic fibers" (Harvey-Gibson, 1897; Mital, 1969), "fibrous epidermal cells" (Mukhopadhyay & Sen, 1986), or "sclerotic warty cells" (Satake, 1934). Dahlen (1988) has pointed out that since these cells gave a negative result for the presence of lignin, they were better referred to as "warty fibers." Similar cells are known in several fern groups and have been discussed in Pteris by Wagner (1978). In these groups various terminologies have been also proposed. Wagner (1978) has suggested the term "venuloid idioblasts" for "structures of various forms and homologies which produce the illusion of tiny veinlets scattered in the interveinal, submarginal, or sinus regions of the lamina." I agree with the use of this term. Unfortunately, as already discussed by Mukherjee and Sen (1981), some authors, when describing these cells in Selaginella, have mistaken them for true veins. In addition, Selaginella, with only two exceptions reported by Wagner et al. (1982), and the extant lycopod genera have only a single vein. Thus, I prefer the term "idioblast," following usage in Mickel and Beitel (1988) and Valdespino (1992, 1993b).

Idioblasts are usually hyaline, have thick walls, and frequently have papillae on the upper surface. Idioblasts may occur individually throughout the surfaces (Figs. 2A, C, E & G; 3F & G), in pairs (Fig. 2B), or as extensive patches. The latter pattern is readily observed in specimens of S. muscosa and in S. moritziana

var. elongata. In S. porphyrospora, the upper and/or lower surfaces of the lateral leaves have one or two, very large idioblasts, which are commonly referred to as "false veins." These idioblasts are larger than in any of the other species here treated, and are very useful to separate S. porphyrospora from S. bernoullii. Similar idioblasts are found in several Old World species of Selaginella (Mukherjee & Sen, 1981). Idioblasts, in general, have a wide distribution within neotropical species of subg. Heterostachys and represent a reliable taxonomic character to distinguish species, as has been shown by Dahlen (1988) working with Hong Kong species of the genus.

The papillae on idioblasts, polygonal, and elongate cells are arranged in 1-3 rows (Figs. 3B, F, & G) or randomly (Figs. 2F; 3A, C-E) (Dahlen, 1988; Gopalakrishnan & Ravi, 1990; Harvey-Gibson, 1897; Mukhopadhyay & Sen, 1986; Somers, 1978) and are either free or interconnected (Figs. 2B & G; 3B).

In Figures 2B, G & H; 3A-G, papillae found on the upper surface of the idioblasts and on similarly elongated marginal cells are more "luminous" due to differences in the electron density recorded on the micrographs. Bienfait and Waterkeyn (1974) have determined that papillae initially accumulate callose, but become silicified with time. Thus, the differences in electron density observed, which result in more "luminous" papillae, are apparently caused by the accumulation of silica in these projections.

Stomata are anomocytic and found mostly in the abaxial surface of all leaf types (Gopalakrishnan & Ravi, 1990; Jermy, 1990), although in some species they

are also located on the adaxial surface of the leaves. On the median leaves they are usually restricted to the medial region along the midrib (Fig. 3A), but in some species stomata, although principally medial, are also scattered throughout, or near the margin along the lower half of the outer base, or even on the margin itself. On the lateral leaves, stomata are mostly restricted to the lower surface, usually along the midrib (Fig. 2H; 3F & H), in the margin (Fig. 2F); however, they can be scattered over the entire surface. These observations generally agree with previous studies of stomatal distribution in Selaginella (e.g., Buck & Lucansky, 1976; Dahlen, 1988; Gopalakrishnan & Ravi, 1990; Harvey-Gibson, 1897; Mital, 1969; Mukhopadhyay & Sen, 1986, Satake, 1934; Somers, 1978).

### III.3. LEAF TERMINOLOGY

The terms used in the descriptions referring to the leaves were adopted following previous usage or for convenience or for their simplicity. In some cases they may have a slightly different connotation than in the past. Some of the terms used here are represented in figures 2C-E, 3B, and 4, and are discussed as follows:

1) "Axillary leaves" refers to those leaves found on the ventral side shortly below each branch dichotomy of the stem. Some authors (e.g., Schoute, 1938) prefer to give them a different term, "angular leaves." Most descriptions of Selaginella species since Spring (1849) and Hieronymus (e.g., 1902, 1904), however, used the term "axillary leaves" as defined here, and thus it has been retained. These leaves generally have the same epidermal and morphological

characteristics as the lateral leaves, although in some species they may be quite different morphologically from the lateral leaves, particularly on branches away from the main stem. According to Schoute (1938), axillary leaves are lateral leaves that have been slightly displaced to the axil of a branch fork.

2) "Median leaves" are located on the dorsal surface of the stem (Dahlen, 1988; Jermy, 1985; Quansah, 1989; Valdespino, 1992, 1993a, 1993b, 1994). "Lateral leaves" are inserted in a lateral to latero-ventral position or in the ventral side of the stem. Some authors (e.g., Harvey-Gibson, 1897) have used the term "dorsal leaves" for median leaves and "ventral leaves" for lateral leaves.

3) For sporophylls I follow Quansah (1989) and designate the ones that are located in the same plane as the median leaves as "dorsal sporophylls" and those located in the same plane as the lateral leaves as "ventral sporophylls." Alternatively, these could be called "upper sporophylls" and "lower sporophylls," respectively. The terms "sporophylls" (Crabbe & Jermy, 1976: 259), "megasporophylls," and "microsporophylls" (Jermy, 1985: 549-551) do not convey any information about size, dimorphism, and relative location of both sporophylls and sporangia on the strobilus. I consider these characteristics of the sporophylls important taxonomically. During this study it was generally observed that the dorsal sporophylls were microsporangiate (and therefore microsporophylls) and the ventral sporophylls were megasporangiate throughout the strobilus (and therefore megasporophylls) or the ventral sporophylls contained intermixed microsporangia and megasporangia. In general, ventral sporophylls are of a smaller size and

morphologically dissimilar to the larger, dorsal sporophylls (see Fig 4, species descriptions and discussion on strobili).

4) Taking into consideration the position and orientation of the median leaves (which are ascending and parallel to the stem) and of the lateral leaves (which are spreading and perpendicular to the stem), their halves, as divided by the midrib, have been designated in the following manner: a) for the median leaves, "outer half" refers to the half of the leaf away from the middle of the stem, and "inner half" to the half of the leaf immediately next to or resting over the middle of the stem. Accordingly, the margins and bases of both halves of the leaf have been designated as "outer margin" and "inner margin," and "outer base" and "inner base;" b) for the lateral leaves, "acroscopic half" refers to the side oriented toward the apex of the stem or branch, and "basiscopic half" to the side oriented toward the base of the stem or branch. Accordingly, the margins and bases of both halves of the leaf have been designated as "acroscopic margin" and "basiscopic margin," and "acroscopic base" and "basiscopic base." Some authors (e.g., Alston et al., 1981; Crabbe & Jermy, 1973, 1976; Dixit, 1992), however, refer to the acroscopic half of lateral leaves as "inner half" and to the basiscopic half as "outer half." I believe their terminology to be incorrect and misleading, particularly for botanists not familiar with Selaginella. Somers (1978) used the terms "upper" and "lower" halves, margins, and bases of the lateral leaves, which although not precisely correct are preferable to the ones just cited above. Jermy (1985) has used the same terminology employed here.

### III.4. STROBILI

In Selaginella there are three basic types of strobili: a) cylindrical with radial symmetry, b) quadrangular with radial symmetry, and c) dorsiventral with bilateral symmetry (Figs. 1B; 4). In the first type, sporophylls are spirally arranged along the axis of the strobilus. This type is characteristic of homophyllous species in subg. Selaginella. In the second and third types, sporophylls are decussately arranged in alternating verticils along the axis of the strobilus. This arrangement is characteristic of homophyllous species in subg. Ericetorum and subg. Tetragonostachys, and of heterophyllous species in subg. Stachygynandrum and subg. Heterostachys. The second type of strobilus, however, is indicative of subgenera Ericetorum, Tetragonostachys, and Stachygynandrum, whereas the third type of strobilus is typical of subg. Heterostachys.

The dorsiventral type of strobilus, as already mentioned in the Introduction, is further characterized by being composed of dimorphic sporophylls. The larger, dorsal, green, and spreading sporophylls are located in the same plane as the smaller, vegetative median leaves, and have a "laminal flap" (Figs. 2D; 4C). The smaller, ventral, hyaline to greenish hyaline, and ascending sporophylls are located in the same plane as the larger, vegetative lateral leaves, and usually do not have a developed "laminal flap". Some authors (e.g., Baker, 1883, 1887; Jermy et al., 1967; Jermy, 1985; Mukhopadhyay & Sen, 1981; Mukhopadhyay & Sen, 1986; Quansah & Thomas, 1985) use the term "resupinate" to designate this type of strobilus. This term implies an inversion of the "normal" heterophylly of the

vegetative stem (in which the smaller, median leaves are dorsal and the larger, lateral leaves are lateral, latero-ventral, or ventral) by a twisting of the fertile axis of the stem. Jermy et al. (1967) asserted that this "resupinate" condition occurred as a result of a 180° "twist" of the stem. Goebel (1905) objected the use of the term resupinate, commenting that "there is no torsion of the flower-axis [strobilar axis]." He suggested instead that the dorsiventral strobilus and dimorphic sporophyll condition arose as an adaptation of the dorsal sporophylls. According to Goebel (1905), the dorsal sporophylls acquired a protecting function of the whole strobilus, which in addition has resulted in an increased capacity of assimilation by these sporophylls. This is to say that the dorsal sporophylls increased in size to protect the sporangia subtended by them as well as the ventral sporophylls.

In order to explain the present-day situation, according to the first hypothesis (resupinate hypothesis), we must assume that the fertile axis originally had the same heterophyllous condition as the vegetative stem and that the following evolutionary changes occurred: a) The fertile axis of the stem twisted 180°. If this were the case, then it would be reasonable to expect some kind of external or internal morphological or anatomical change in that region of the stem that would indicate such twist. b) As a consequence of this twist, the "originally" larger, ventral sporophylls would have become the dorsal sporophylls, and its lower (abaxial) surface (which must have been similar to that of the lateral, vegetative leaves, see discussion on the Leaf Epidermis section) would have become now the

upper surface, and vice versa. This change requires, in turn, that the elongate cells of the lower surface changed to become polygonal and photosynthetic in their new position as the upper surface, and vice versa for the polygonal cells of the "original" upper surface. These changes would have resulted in a condition that resembles that found on the median, vegetative leaves. c) The opposite transformation would have then occurred on the "original" smaller, dorsal sporophylls, where they have now become the ventral sporophylls, and their upper surface became the lower surface. In this case the polygonal, photosynthetic cells of the upper surface would have to become elongate and hyaline or greenish hyaline (i.e., with diminished photosynthetic capabilities); no changes, however, would be required for the "original" lower surface (see discussion below). My examination of strobili from neotropical and some Old World species of subg. Heterostachys fails to reveal any morphological or probable anatomical evidence that a twist of the fertile axis, as required by this hypothesis, has indeed occurred. On the other hand, Goebel's (1905) hypothesis does not require any change on the stem, and only requires minor changes on the sporophylls. In the simplest scenario for this hypothesis, the larger, dorsal sporophylls of species with dorsiventral strobili (i.e., subg. Heterostachys) originated from the dorsal sporophylls of heterophyllous species with quadrangular strobili (i.e., subg. Stachygynandrum). According to Goebel's hypothesis the following evolutionary changes would have occurred: a) the lamina of the "original" dorsal sporophylls would need only to expand and maintain the same epidermal characteristics (i.e.,



having polygonal, photosynthetic cells on the upper surface), and b) the lamina of the ventral sporophylls would have only to be reduced in size (in some cases with major tissue reduction) and retain the same epidermal pattern as in the ancestral condition. Extant species of subg. Stachygynandrum and subg. Heterostachys, have, in general, both surfaces of the ventral sporophylls composed of elongate cells.

It is clear that Goebel's (1905) hypothesis involves minor morphological and no anatomical changes; from an evolutionary point of view it is more parsimonious. In support of his hypothesis, Goebel (1905) explained that "if an inverse-dorsiventral flower [a dorsiventral strobilus] should grow out vegetatively, the outgrowth assumes the dorsiventrality of the "original" vegetative shoot, so that the "inversion" of the dorsiventrality was only caused by the formation of the flower [strobilus]." I have observed the same vegetative growth from the apex of dorsiventral strobili in species of subg. Heterostachys (e.g., S. correae, S. finitima, S. porphyrospora, S. tenella), and in both homophyllous and heterophyllous selaginellas (Valdespino, 1993a, b) with "reversion" to the "original" condition of the vegetative stem. I am, therefore, more inclined to accept Goebel's hypothesis, rather than the resupinate one. I believe, however, that the larger, dorsal sporophylls are more protective of its sporangia, rather than of the whole strobilus (other possible adaptive functions are discussed below). I am also somewhat skeptical of the second function of the dorsal sporophylls proposed by Goebel (1905). As discussed below, a portion of the dorsal sporophyll develops into a

laminal flap, which is usually hyaline to greenish hyaline, and thus the putative increment in the capacity of assimilation [photosynthesis?] may not be very substantial after all.

Ventral sporophylls are usually smaller than the dorsal sporophylls, they have the laminal tissue very much reduced, frequently have larger marginal projections (i.e., cilia) than the dorsal sporophylls, lack a developed "laminal flap," have both surfaces composed of usually hyaline or greenish hyaline, elongate cells, and are ascending and located in the same plane as the larger, lateral, vegetative leaves.

#### III.4.1. LAMINAL FLAP

In species of subg. Heterostachys, dorsal sporophylls have a "pseudo-appendage" on the adaxial surface. This pseudo-appendage has received considerable attention by recent workers. Mukhopadhyay and Sen (1981) have described it as "a laminal flap, developed as a vertical projection on the adaxial surface of sporophylls or bracts."<sup>1</sup> They believe it to be a continuation of the lamina, i.e., a new structure developed perpendicular to the adaxial surface of the dorsal sporophylls and situated next to the ligule. Quansah and Thomas (1985)

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<sup>1</sup> I conclude that their usage of the term "bracts" refers to sterile sporophylls, most likely, dorsal sporophylls. In a more recent paper, Mukhopadyay and Sen (1986) stated that the laminal flap occurs only on the adaxial surface of the larger sporophylls [which are always the dorsal sporophylls] of taxa with heteromorphic sporophylls. This seems to support my interpretation of their earlier usage of the term "bracts."

examined 133 species of Selaginella from Africa and America, and they found in many of them the same laminal flap described earlier by Mukhopadhyay and Sen (1981). Although they were aware of the previous term given to this structure by Mukhopadhyay and Sen (1981), Quansah and Thomas (1985) decided to rename it "sporophyll-pterix." Both groups of authors, however, apparently overlooked the fact that Goebel (1905), almost a century earlier, had already described the same structure and referred to it as "a wing-like appendage," and that Gena et al. (1979) had taken note of this structure, which they termed "adaxial keel or flap." Goebel (1905) considered this structure an outgrowth of the back [upper surface along the midrib region?] of the dorsal sporophylls. He concluded that this structure served to protect the sporangia. Although, to my knowledge, Goebel's term is the earliest over the other three proposed, I believe that a more useful term to describe this structure, once properly defined, is that proposed by Mukhopadhyay and Sen (1981). Hereafter I will refer to this structure as the laminal flap. Quansah and Thomas (1985) suggested that the laminal flap was the result of a fold of the outer half<sup>2</sup> of the sporophyll [dorsal sporophyll] onto the adaxial surface of itself. After

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<sup>2</sup> It is very difficult to determine which, if any, of the two margins of the sporophylls should be referred to as "inner" or "outer" half, because the sporophylls are attached to the fertile axis by the central part of their bases. As a result, both margins are equidistant to the axis. In addition, both halves of the dorsal sporophylls take part in the formation of the laminal flap, although the one bearing the projection does it more. I propose here that by convention, we refer to the half that does not have the projection (laminal flap) as acroscopic half, and to the one that has the projection (laminal flap) as basiscopic half. In this way, I believe, it would be easier to establish future comparisons of the laminal flap among species from different regions of the world. Accordingly, I will use the term basiscopic half.

observing the laminal flap in all neotropical taxa and some Old World species of subg. Heterostachys, I consider it is proper to define the laminal flap as "a laminal projection on the dorsal sporophylls that results from the partial fusion of the epidermal tissue of the adaxial surface of these sporophylls. This projection is in fact the basispic margin of the dorsal sporophylls that is more or less perpendicular to the adaxial surface." As a result of this partial fusion and the new position of the basispic margin, the portion of the sporophylls that becomes fused runs along the midrib, but at different lengths of it. The edges of this region, which may be termed "keel" (Fig. 2D), frequently have projecting hairs or cilia, which make this region appear to be the basispic margin. This false basispic margin was apparently interpreted by Mukhopadhyay and Sen (1981) as the true margin, and they considered the laminal flap as a new structure developing on the adaxial surface and along the midrib of the dorsal sporophylls. It is clear, however, that the laminal flap is not an appendage or structure developed de novo, but a modification of the basispic margin.

Quansah and Thomas (1985) have classified the laminal flap (as sporophyll-pterix) into two kinds, the "complete laminal flap," which occurs from the apex along about two-thirds the length of the midrib, then extends obliquely to the edge of the basispic side, as far as the base of the sporophyll," and the "partial laminal flap," which occurs from the apex along about one-third the length of the midrib, then extends obliquely to the edge about midway along the length of the basispic side of the sporophyll." It is clear, however, that both the "partial" and "complete"

laminal flap are only expressions of the same character.

Interestingly, in Quansah and Thomas' (1985) investigation most of the species treated in this monograph were found to have either "partial" or "complete" laminal flap (see Table II, in Quansah & Thomas, 1985: 51). My observations on the laminal flap of the species treated in this monograph, in general, agree with the results presented by Quansah and Thomas (1985).

The fact that species with dorsiventral strobili from Africa (Quansah, 1989; Quansah & Thomas, 1985), America (Quansah & Thomas, 1985; Valdespino, 1993b, and herein), India (e.g., Gena et al., 1979; Dixit, 1992), the Pacific region (Jermy, 1985), and other regions, have laminal flaps, suggests that this structure is taxonomically useful to define subg. Heterostachys.

Figure 2. A-H. *Selaginella hyalogramma* sp. nov. (Davidse & González 21525,

MO). A. Upper surface of a median leaf; note idioblasts (id). B. Detail of the upper surface of the same leaf; note single papilla on a rounded cell (pa), the stomata (st) in a medial and marginal to submarginal position (indicated by the arrows), and single or paired idioblasts (id); note interconnected papillae on paired idioblasts. C. Upper surface of a median leaf; note the outer margin (om), the inner margin (im), and idioblasts (id). D. Dorsal sporophyll; note the laminal flap (lf) and the keel (ke). E. Upper surface of a lateral leaf; note the acroscopic margin (am), the basisopic margin (bm), and idioblasts (id). F. Detail of the basisopic margin of the same leaf showing very short, marginal to submarginal hairs (h), marginal stomata (st), and papillae on rounded cells (pa). G. Detail of the upper surface of a lateral leaf; note rounded to polygonal cells with sinuate walls, and idioblasts. H. Detail of the lower surface of a lateral leaves; note elongate cells with sinuate walls, idioblasts, and stomata along the midrib. (Scale bar: A, D, & E = 500  $\mu\text{m}$ , and for F = 50  $\mu\text{m}$ ; B, G, & H = 100  $\mu\text{m}$ ; C = 100  $\mu\text{m}$ ).

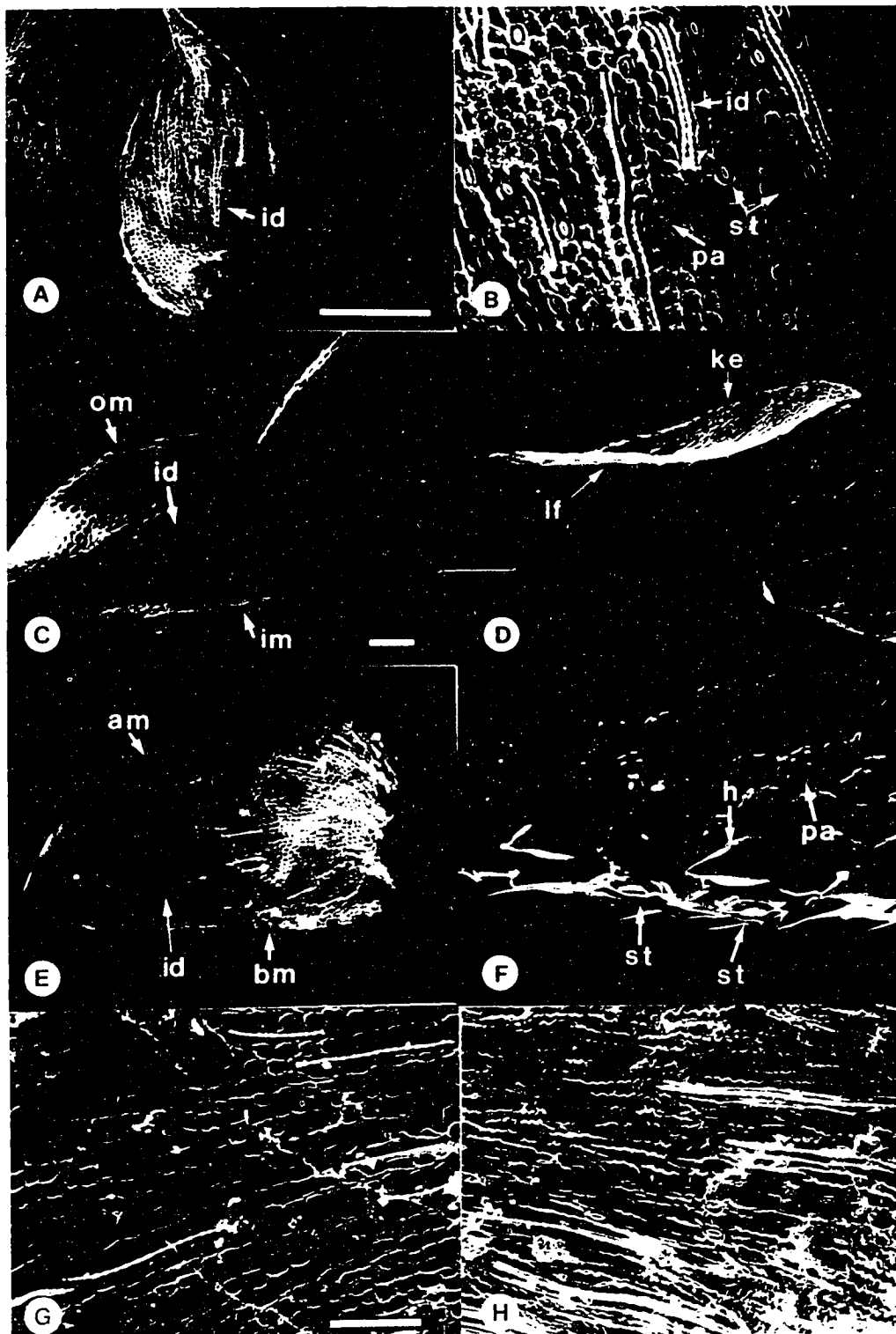


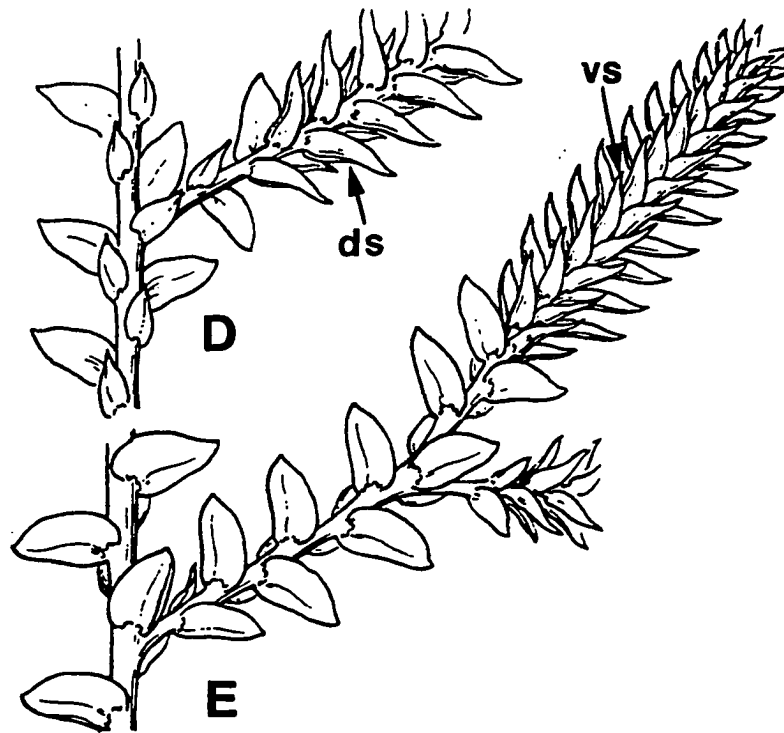
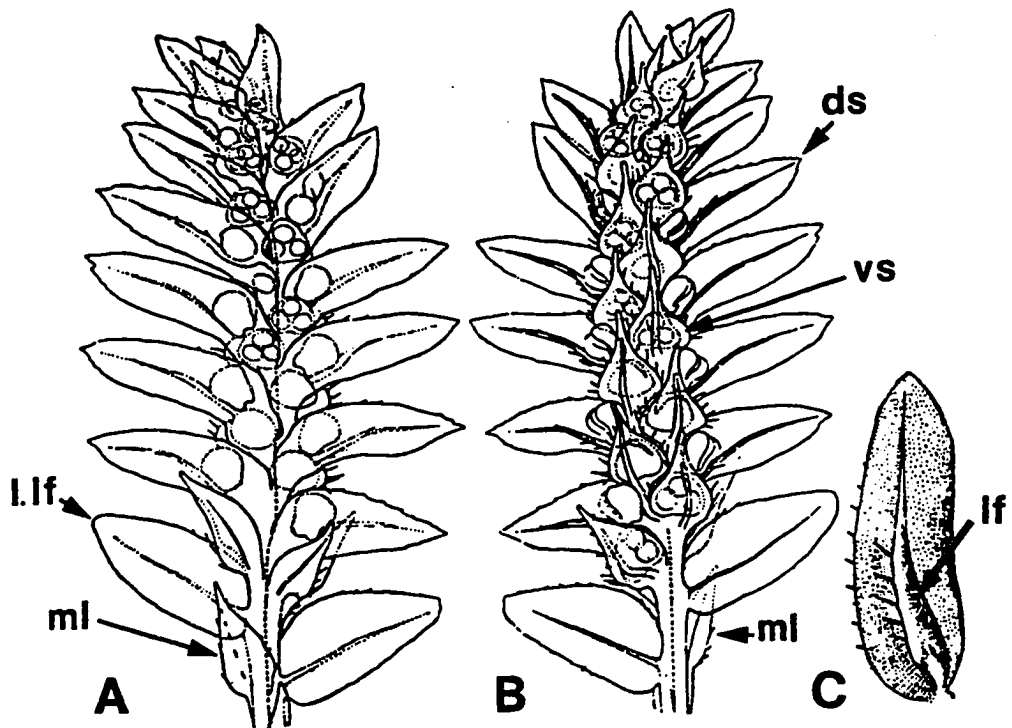
Figure 3. Detail of the upper and lower surfaces of median and lateral leaves of Selaginella cavifolia (A, B, D, F & G: Alston 7413, US) (C, E & H: Acosta-Arteaga 309, COL). A. Detail of the upper surface of a median leaf; note stomata (st) along the midrib, rounded cells with sinuate outline (so), and papillae on rounded cells. B. Detail of the inner margin (im) of a median leaf; note interconnected (ip) and free papillae (pa) on the elongate, marginal cells (emc). C. Detail of the upper surface of a median leaf; note rounded cells (rc) with many papillae per cell (pa). D. Detail of the upper surface of a median leaf; note the smaller cuticular projection (cp) on rounded cells, and many papillae per cell. E. Detail of the upper surface of a lateral leaf; note rounded to polygonal cells (rc), some with many papillae per cell. F. Detail of the lower surface of a lateral leaf; note elongate cells with sinuate walls, idioblasts (id) with 2-3 rows of papillae, and stomata along the midrib. G. Detail of previous micrographs; note elongate cells with sinuate walls (ec), and idioblasts (id) with 2-3 rows of papillae. H. Detail of the lower surface of a lateral leaf showing a close-up of the stomata (st) along the midrib. (Scale bar: A & H = 50  $\mu\text{m}$ ; B & D = 10  $\mu\text{m}$ ; C = 25  $\mu\text{m}$ ; E, F & G = 100  $\mu\text{m}$ .).





Fig. 4. Strobilus morphology of two species of Selaginella subg. Heterostachys.

A-C. Selaginella chrysocaulos (Old World tropics). A. Upper surface view of the dorsiventral strobilus; note median leaf (ml), lateral leaf (l.lf), and larger, dorsal sporophylls in the same plane as the median leaves. B. Lower surface view of the dorsiventral strobilus; note median leaf (ml), dorsal sporophylls (ds), and smaller, ventral sporophylls (vs) in the same plane as the lateral leaves. C. Detail of a dorsal sporophylls; note part of the adaxial tissue fuse to form the laminal flap (lf). D & E. Selaginella popayanensis (New World tropics). D. Upper surface view of part of the main stem and strobilus; note dorsal sporophylls (ds) in the same plane as the median leaves. E. Lower surface view of part of the main stem and strobilus; note ventral sporophylls (vs) in the same plane as the lateral leaves. (A-C, slightly modified from Goebel, 1905; D & E, slightly modified from Mickel & Beitel, 1988).



## CHAPTER IV

### CYTOLOGY AND APOGAMY

#### IV.1. A REVIEW OF CYTOLOGICAL WORK IN *SELAGINELLA*

Cytological work on the genus Selaginella has been based on somatic chromosome counts of approximately 106 species (Takamiya, 1993). These studies indicate that the genus is characterized by low base chromosome numbers,  $x = 7, 8, 9, 10, 11, 12$ , forming an aneuploid series. Additionally, triploids, tetraploids, and hexaploids are known (Jermy et al., 1967; Jermy, 1990; Kuriachan, 1963; Löve et al., 1977; Takamiya, 1993). This wide cytological variation in Selaginella is perhaps an adaptation to different environmental and ecological conditions (Jermy et al., 1967).

The only chromosome counts of neotropical species of subg. Heterostachys have been made by Jermy et al. (1967). I have been able to examine vouchers used for their counts and redetermined some of them. For discussion purposes they are listed here as follows: S. broadwayi (Jermy 3089 K!), S. flagellata (as S. broadwayi, Jermy 2281 K!), S. muscosa (as S. hartii Hieron., Jermy 2102 K!; as S. cladorrhizans A. Braun [= S. tenella (P. Beauv.) Spring], Jermy 2559 K!), S. muscosa vel aff. (as S. trifurcata Baker, Jermy 3119 K!), S. porelloides (Jermy 2302 K!), and S. stenophylla (apparently from cultivated material; not seen by me). According to Jermy et al.'s (1967) data, the chromosome numbers of some of these species fall into the basic numbers of  $x = 9, 10$ , and two species have an

unknown basic chromosome number (i.e., S. porelloides with  $2n = 36, 40$  and S. stenophylla with  $2n = 50, 60$ ). Selaginella broadwayi and S. flagellata are diploids,  $x = 10$ , and S. muscosa, has two somatic numbers,  $2n = 18$  and  $20$ . This discrepancy in basic numbers may be explained by aneuploid changes either by centric fusion or fission. This mechanism of aneuploidy has been suggested for some Japanese species of Selaginella with basic chromosome number of  $x = 8$  and  $9$ , and for which karyotype is known (Takamiya, 1993). Alternatively, this discrepancy may be the result of a mistake in the counts reported by Jermy et al. (1967), perhaps due to the small size of the chromosomes found in Selaginella. Similarly, chromosome counts that reported a basic number  $x = 11$  for S. pallescens (C. Presl) Spring [as S. cuspidata (Link) Link] (Tchermak-Woes & Dolezal-Janish, 1959) and for S. tamariscina (P. Beauv.) Spring (Tsai & Shieh, 1988), have been suggested by Jermy et al. (1967) and Takamiya (1993), to be "doubtful."

The most comprehensive review of previous cytological work conducted in Selaginella has been given by Takamiya (1993). Takamiya (1993) also provided new somatic chromosome counts for 16 native and cultivated species in Japan, in addition to an interesting karyomorphologic analysis of the data. In his study the closely allied species S. helvetica (L.) Spring and S. nipponica Franch. & Sav. have a basic chromosome number of  $x = 9$ , yet they have different karyotypes. According to Takamiya (1993), S. helvetica has medium length chromosomes with the karyotype type  $x = 9 = 4m + 2sm + 3(st + t)$ , whereas S. nipponica shows

$\underline{x} = 9 = 3m + 6(st + t)$ . On the other hand, S. heterostachys Baker, the type of subg. Heterostachys, is shown to be a tetraploid species with  $\underline{x} = 8 = 4m + 4(st + t)$ . This karyotype is also shared by S. boninensis Baker. Takamiya (1993) indicated that these two species have similar general (fide Iwatsuki, 1992) and megaspore (fide Minaki, 1984) morphologies. Because of these similarities, he suggested that S. heterostachys might be a tetraploid derivative of S. boninensis. My examination of herbarium material of S. heterostachys, deposited in NY, confirms that this species is indeed a member of subg. Heterostachys. I have not seen herbarium material of S. boninensis, but examination of a close-up photograph of a strobilus of this species, found in Nakaike (1982: 35), and comparison of it with those of S. heterostachys from herbarium material and a close-up photograph from the same source (Nakaike, 1982: 38), reveals that the former species is also a member of subg. Heterostachys. Thus, Takamiya's results support a relationship between two members of subg. Heterostachys in Japan. The other member of subg. Heterostachys, S. lutchuensis Koidzumi, showed a different basic chromosome number of  $\underline{x} = 9$  with karyotype  $\underline{x} = 9 = 3m + 6(st + t)$ . According to Takamiya's (1993) data, this is the same formula found in other species such as S. doederleinii Hieron., S. helvetica, S. limbata Alston, and S. selaginoides, which are not closely related to S. lutchuensis or to the other two species of subg. Heterostachys studied by him. Furthermore, none of these four species are in fact closely related to each other.

To summarize, although chromosome numbers and karyomorphologic

patterns may be characteristic of some species, sometimes even of related species, Takamiya's data do not seem to support relationships among closely related taxa, i.e., the three species of subg. Heterostachys studied by him. The same pattern may be found in totally unrelated species. Takamiya (1993) concluded that "No clear association is found between the basic chromosome number and subgeneric classification." A similar conclusion was reached by Jermy et al. (1967). It seems, therefore, that basic chromosome numbers and karyomorphology are not very useful taxonomic characters in the genus Selaginella (Jermy, 1967; Takamiya, 1993), as they are in ferns (e.g., Walker, 1973).

#### IV.2. APOGAMY

The genus Selaginella exhibits a life cycle characterized by the alternation between gametophytic and sporophytic generations. Selaginella, despite its ancient lineage, has about 700 species and appears to be undergoing speciation (Dixit, 1992; Webster, 1992). Most of the species, with very few naturally occurring exceptions, are restricted to particular geographic areas. Within these geographic areas, however, some of the species are widely distributed. In this study species such as S. flagellata, S. minima, S. muscosa, S. porelloides, and S. simplex proved to have some of the widest distribution patterns of any selaginellas in the Neotropics. All five species have in common the fact that their strobili are frequently wholly mega- or microsporangiate. In the case of wholly megasporangiate strobili, there may be but a few microsporangia, usually at the tip

of the strobilus, and in the case of wholly microsporangiate strobili they may have only very few megasporangia scattered throughout the strobilus. In Selaginella this sporangial distribution seems to be common, based on the sporangial distribution studies that have been carried out (Dahlen, 1988; Fraile & Riba, 1981; Horner & Arnott, 1963; Quansah, 1988; Zamora et al., 1992). These studies have all reported sporangial patterns the same as the ones described above. The megasporangiate condition of the strobilus has been usually associated with some kind of "disruption," such as apogamy, in the normal life cycle of Selaginella species (Dahlen, 1988; Kornaś & Jankun, 1983).

Apogamy can be defined as a process in which a sporophyte develops directly from the gametophyte without fertilization (Bower, 1939; Goebel, 1905). Indeed, studies by Kornaś and Jankun (1983) on S. tenerrima A. Braun ex Kuhn, an African member of subg. Heterostachys, and by Goebel (1915, fide Ruf, 1976) and Geiger (1934, fide Ruf, 1976) on the neotropical S. muscosa (as S. anocardia) have shown that spores from wholly megasporangiate strobili are capable of developing new sporophytes without fertilization (i.e., apogamously). Cronquist (1988) has asserted that often apomixis is associated with polyploidy and interspecific hybridization. Interestingly, Kornaś and Jankun (1983) also reported that S. tenerrima was a triploid species. Dahlen (1988) has also reported that in specimens of S. ciliaris (Retz.) Spring, a member of subg. Heterostachys from Hong Kong, all the strobili examined were megasporangiate. Both Dahlen (1988) and Kornaś and Jankun (1983) have suggested that because of this



megasporangiate condition, S. ciliaris was probably apomictic. This species, however, has been indicated as being diploid by Jermy et al. (1967). Thus, apogamy or the megasporangiate condition of the strobilus may not necessarily be the result of polyploidy. There must be some other underlying factor(s), probably involving some endogenous mechanism by which heterospory is regulated in Selaginella. In this regard, Brooks' (1973) study sheds some light. He was able to influence the production of sporangia in strobili of S. wallacei Hieron., a member of subg. Tetragonostachys, to produce almost exclusively mega- or microsporangiate strobili by spraying clumps of this plant with either 2-chlorethylphosphonic acid or Ethepon (an ethylene-releasing compound). Furthermore, when he sprayed plants of S. pallescens (C. Presl) Spring, a member of subg. Stachygynandrum, with Ethepon it caused the production of megasporangia in the sporophyll rows that, because of their position on the axis of the strobilus, would normally produce microsporangia. He suggested that the endogenous mechanism regulating heterospory in Selaginella might be influenced by hormones, particularly ethylene. It seems that two mechanisms, apogamy and hormones, acting individually or perhaps in combination, or one as the result of the other, are involved in the formation of megasporangiate strobili in Selaginella.

In pteridophytes, apogamy has often been considered an adaptation to xeric environments, because it allows the formation of a new plant without the intervention of water (a critical factor for fertilization to occur in pteridophytes) and without a prolonged gametophytic phase (Kornaś & Jankun, 1983). This

would presumably protect the plant from the hostile environment, but at the same time would allow its reproduction. Geiger (1934) has shown, however, that in S. muscosa (as S. anocardia) apogamy was dependent on a very moist and shady environment. Indeed, I have observed S. muscosa growing on the very humid slopes of the Floresta da Tijuca in Rio de Janeiro, Brazil. Chromosome counts in this species have shown two different basic chromosome numbers, indicating the existence of polyploid populations. These polyploid populations may have originated by apogamy, as has been demonstrated in S. tenerrima by Kornaś and Jankun (1983). It appears, therefore, that in Selaginella apogamy may be facultative rather than obligate.

In Selaginella, there are other possible advantages derived from the apogamous condition. I have discussed some of these advantages in the species descriptions of S. minima, S. muscosa, and S. porphyrospora. However, they can be summarized as follows: a) it provides the opportunity for wider or long-distance dispersal by requiring, at least theoretically, a single spore from one spore type (in this case a megaspore) to be dispersed, either by abiotic factors (e.g., rain) or by biotic factors (e.g., animals)<sup>3</sup>, and b) upon landing in a favorable site, this megaspore can germinate and establish a new population with the same genetic makeup of the parent population. At the same time, the new population provides

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<sup>3</sup> A recent paper by Mound et al. (1994) provides a review of the insect fauna associated with species of Selaginella. It seems that at least 19 species from six different orders of insects breed on some species of Selaginella. Although there is no concrete evidence, it is entirely possible that since these insects are in close contact with plants of Selaginella, they may in turn serve as dispersal agents.

the possibility for future evolutionary divergence through mechanisms such as geographic isolation. Alternatively, successful gene flow between the newly establish population and the parental, sexual population or any other sexual population of the species, will increase the diversity of the gene pool of the species. Cronquist (1988) has summarized the potential evolutionary effect of apogamy thusly: "There may be enough sexual reproduction to keep the pot bubbling, and enough apomixis [in our case apogamy] to permit any fortuitously formed, highly competitive genotype to maintain itself without change. Interspecific hybrids and hybrid segregates can thus reproduce with a minimum of meiotic hazards, while still retaining the capacity to throw an occasional potentially stable new genotype." This seems to be a rather distinct possibility when we consider that S. tenerrima is widely distributed in Africa, persisting from year to year, most probably, only by apogamy (Kornaś & Jankun, 1983), and without or with very sporadic sexual reproduction. Perhaps it exists as both a sexual and an apomictic species (i.e., apogameon). Therefore, we may reasonably expect that for the neotropical species of subg. Heterostachys that exhibit a wide distribution pattern, and for which a megasporangiate strobilar pattern has been established, apogamy may be occurring. In fact, this seems to be the case for I have observed specimens from the same region or even the same locality some of which have both mega- and microsporangiate strobili and others have only wholly megasporangiate or microsporangiate strobili. This is particularly characteristic of e.g., S. flagellata and S. porphyrospora.

Finally, Ruf (1976) has provided a very informative review of the occurrence of apogamy in several Selaginella species in his unpublished doctoral dissertation.

## CHAPTER V

### SURVEY OF SPORE MORPHOLOGY WITH EMPHASIS ON MEGASPORES

#### V.1. INTRODUCTION

Hellwig (1969) and A. Tryon (1949), both using light microscopy (LM), demonstrated that spore color and sculpturing patterns were valuable taxonomic characters for species distinction. The scanning electron microscope's (SEM) greater resolution allows more detailed comparison than LM, especially in determining sculpturing and microstructure patterns in Selaginella species (Buck, 1977; Dahlen, 1988; Mickel & Valdespino, 1992; Morbelli, 1977; Sharma et al., 1989; Valdespino, 1992, 1993b), which have been shown to be critical in assessing species groups (Somers, 1978; A. Tryon & Lugardon, 1991).

Most SEM studies of spore morphology in Selaginella have been conducted using air-dried or herbarium samples of untreated spores. The acetolysis technique, which is commonly used in palynological studies (Lynch & Webster, 1975, and references therein), has been avoided for the most part. This technique has been shown to cause rupture and disintegration, as well as expansion of the perispore in some pteridophyte genera (Large & Braggins, 1990). According to Lynch and Webster (1975) the acetolysis technique also has some marked disadvantages for the study of pollen of living taxa, because it causes pollen grains to collapse in the vacuum chamber of the SEM, and in other cases results in the

loss of significant information related to the ornamentation of the pollen grain. In addition, the acetolysis technique generally involves many more preparatory steps prior to observation with the LM or SEM, than direct methods (e.g., Lynch & Webster's method, 1975) of spore and pollen observation. The acetolysis method was not employed in this study.

## V. 2. SPORE MORPHOLOGY STUDIES IN *SELAGINELLA* SUBG. *HETEROSTACHYS*

Spore sculpturing and microstructure patterns are helpful characters to distinguish among closely related taxa or species complexes in *Selaginella*. This is particularly true when more traditional morphological characters fail to clearly separate species.

The sculpturing patterns of the megaspore exospore are readily seen using low magnification (e.g., using a dissecting microscope with 40-70×), while microspores are better observed using a compound microscope. Both types of spores are exceptionally informative when viewed using the SEM. Because megaspores are more readily observed than microspores, I have focused this research on this type of spore. A SEM survey of the megaspore morphology of most of the species and of the microspores from only few selected representative species, believed to represent the variation within taxa, was undertaken. While this study covered most of the neotropical species of *Selaginella* subg. *Heterostachys*, the results reported here concern only those species treated in this monograph (i.e., species from Central and South America).

### V.2.1. OBJECTIVES:

The objectives of this study were to:

A. Survey the sculpturing and microstructure patterns of both spore types in order to determine whether these patterns are characteristic of the taxa examined, and thus whether these patterns could be used as taxonomic characters to separate species in Selaginella subg. Heterostachys.

B. Determine if the spore characteristics of the studied species help define subg. Heterostachys.

### V.2.2. MATERIALS AND METHODS

The procedures for preparing and examining spore samples closely followed standard techniques for LM and SEM, as described by Hellwig (1969), Minaki (1984), and Somers (1978).

Megaspore and microspore samples were taken from herbarium specimens, usually from mature sporangia that were about to open in order to avoid mechanical damage of the spores or to sample immature spores. Megaspores were hand-positioned directly onto double-sided adhesive tape affixed to stubs, sputter coated in a Hummer II in vacuum with 10 nm of gold, and viewed with an AMRAY Model 1838 scanning electron microscope at 10, 15, and 20 KV. Microspores were originally treated in the same way, but when observed with the SEM most of them were collapsed either because they were originally collapsed, or became so as result of the vacuum pressure in the sputter coater and the

vacuum chamber of the SEM. Therefore, a slightly modified version of the method proposed by Lynch and Webster (1975) was followed. Strobili samples containing microsporangia (i.e., with microspores) were rehydrated for 24 hrs (or 48 hrs) in 3% Aerosol-OT, washed 3× with distilled water (10 min each), dehydrated in an EtOH series: 50%, 70%, 90%, 100% (2×), and critical point dried. Microsporangia were then removed from the strobili, placed onto a stub covered with double-sided adhesive tape and opened to release the microspores, after which they were coated and viewed the same as were megaspores.

Measurements of the spore diameter, including the equatorial flange when present, were generally made on the proximal face and from about 10 spores taken from one to three specimens. Untreated megaspores were measured with a stereomicroscope (SM) Bausch & Lomb Stereozoom 7, Zoom range 10-70×, and from the SEM micrographs. Microsporangia containing microspores were broken open in one or two drops of 85% lactic acid placed on a glass micro-slide, the microspores were evenly distributed on the slide with a dissecting needle, a cover glass was placed on top of the slide, the slides were then heated for 5-10 seconds over an alcohol burner. This preparation was allowed to cool for 10 minutes and sealed with transparent nail polish, after which observation and measurements were made with a Nikon light microscope (LM) Model L-Ke. Additional measurements, when available, were made from SEM micrographs of the microspores. Both the SM and LM were equipped with ocular micrometers.

SEM micrographs of the proximal and distal faces of the mega- and



microspores, as well as close-ups of both faces of the megaspores were taken. In general, SEM micrographs of the two faces and of the close-ups of the megaspores were taken at (180 $\times$ ) 200 $\times$  and 1500 $\times$  (and occasionally at 3000 $\times$ ) respectively. Micrographs of the microspores were taken at 1000 $\times$ , 1500 $\times$ , 2000 $\times$  (and occasionally at 4000 $\times$  and 5000 $\times$ ). The different magnifications of the micrographs taken are indicated with a scale bar on the figures.

Megaspore color was determined from air dried spores of recent specimens using Ridgway's (1912) color standards. Some variation in the coloration may occur as a result of age, particularly in the case of snow-white megaspores that change to bone-white or cream, therefore spores taken from recent specimens are preferred when determining spore color. The color of the microspores is generally tan to orange and does not vary much among different species. It is not, therefore, considered a useful taxonomic character, and no emphasis was placed on it.

The terminology used to describe spore sculpturing patterns closely follows that of Ferrarini et al. (1986), Kremp (1965), Moore and Webb (1978), and A. Tryon and Lugardon (1991). At the present time there are no adequately standardized terms for the different microstructure patterns observed in Selaginella megaspores (Minaki, 1984). In some instances, and closely following Minaki (1984), when terms normally applied to the "gross" sculpture of the spore serve to describe microstructure patterns, I have use the prefix "micro" in front of them. In this study micrographs, when supplied, are considered the basic reference to

ascertain sculpturing and microstructure patterns rather than descriptions.

Descriptions for the megaspores of most of the species and for microspores of only selected taxa are provided. In addition to descriptions provided here, a slightly abbreviated version has been supplied at the end of the taxon descriptions in the Taxonomic section of this monograph.

### V.2.3. RESULTS AND DISCUSSION

Spores in Selaginella are tetrahedral, tetrahedral-globose, or tetrahedral-ovoid, with a triradiate (trilete) aperture, frequently with an equatorial flange, and have various sculpturing patterns. These sculpturing patterns are formed by projections of the exospore in the form of papillae, reticula, ridges, rugae, verrucae, scabrae, striae, grana, etc. These projections are usually covered by silica deposits (A. Tryon & Lugardon, 1991) forming micro-granulate, micro-papillate, or micro-echinulate "ornamentations."

In general, megaspores of the studied species have the distal face reticulate, either with an open or close reticulate pattern, composed of low or high ridges. These ridges of the reticulum, however, are not as elevated as those described by Somers (1978) for species in series Articulatae. The proximal face is usually smoother since it is the area of contact between the four spores forming the tetrahedral tetrads. It may be reticulate (e.g. S. hyalogramma, Fig. 6E, members of the S. moritziana complex, S. porphyrospora, Fig. 7A), but with a close reticulum, generally composed of lower ridges than those on the distal face.

Megaspore sculpturing and microstructure patterns observed on studied species do not appear to be exclusive of subg. Heterostachys; similar patterns are found in species of subg. Stachygynandrum as illustrated by Hellwig (1969), A. Tryon and Lugardon (1991), and Valdespino (1992, 1993, and unpublished data for members of the groups centering about S. revoluta Baker and S. flabellata Spring). These patterns, however, seem to be consistent within species according to micrographs taken from different collections of the same species (although some exceptions may be encountered, see e.g., S. minima). According to A. Tryon (1986) the structural components of the spore wall in Selaginella show a remarkable stability when extant and fossil spores are compared, lending support to the use of these characters to distinguish taxa.

The megaspores of some species (e.g., S. hyalogramma, S. muscosa, S. porphyrospora) characteristically show a strongly developed equatorial flange (Figs. 6A, C, E & G; 7A & D). In other species (e.g., S. tenella) the equatorial flange may be less developed (Figs. 8A), while others species are characterized by completely lacking an equatorial flange (e.g., S. minima, S. bernoullii, Figs. 5A & C; 7F & I). In some cases the lack of the flange may occur as a result of abrasion, perhaps due to mechanical interaction between spores or due to age (see Fig. 6A & C).

Observation of the distal and proximal faces of the megaspores studied at high magnification (1500× to 3000×) revealed different microstructure patterns and, more interestingly, the presence of small pores. These pores can be termed

"micro-foveolae." The micro-foveolae apparently serve as passage for the structures described by Morbelli and Rowley (1993) as "wicks," structures found in the locular space between the tapetal cells and megaspores of Selaginella, serving to establish contact between the tapetal cells and the plasma membrane of the megaspore cytoplasm. According to Morbelli and Rowley (1993), wicks "appear to be routes for the transport of materials from the tapetum to developing megaspores."

Microspores of the selected taxa studied (e.g., S. flagellata, S. muscosa, S. tenella) are characterized by having spiny, rod-like (i.e., echinate, baculate, clavate), or spheric projections on the distal face (Figs. 9A-F, H & J). In some species (e.g., S. broadwayi, S. minima) these projections are also present on the proximal face (Figs. 9 G & I), while in other species these projections are absent from both faces of the microspore. These projections are frequently "ornamented," primarily with papillae or echinulate projections (Figs. 9A, B, I & J). In S. muscosa it was observed that the clavate projections of the distal face may lose their spheric "heads," thus resembling a baculate projection. In this species it was also observed that the projections may fuse around the equator to form an incipient equatorial flange (Fig. 9D). These different projections apparently help to attach the microspores to the megaspores, thus assuring the probable dispersion of both spore types at the same time.

There was a marked variation in megaspore color, from white and yellow to orange.

The description of the spore sculpturing and microstructural patterns submitted here are generally in agreement with those presented in the comprehensive spore survey of A. Tryon and Lugardon (1991). The terms "close reticulum" and "open reticulum," in the descriptions refer to the relative width of the areola composing the reticulum.

#### V.2.3.1. SPORE DESCRIPTIONS

##### 1. *Selaginella minima* Spring (Figs. 5A-D; 9I & J).

Megaspores snow-white, frequently with a slightly developed equatorial flange or this absent; proximal face rugulate, striate-reticulate to reticulate with open to close reticulum of low ridges, the microstructure coarsely micro-echinulate to micro-papillate or smooth, with micro-foveolae; distal face rugulate to rugulate-reticulate or reticulate with open reticulum of low ridges, the microstructure coarsely micro-echinulate to micro-granular, or smooth and micro-foveolate; 270-350  $\mu\text{m}$  diam. Microspores tan, without an equatorial flange; proximal and distal faces with echinulate, verrucate to gemmate projections over an echinulate microstructure, 45-50  $\mu\text{m}$  diam.

NOTE: The megaspore sculpturing pattern depicted in Figs. 5A-D is somewhat different from that of other specimens examined from Mexico, Brazil, and even from a specimen from the same general area in Panama. The sculpturing pattern of the latter specimens is similar to the one illustrated by A. Tryon and Lugardon (1991: 614-615, Fig. 231.53).

**2. *Selaginella broadwayi* Hieronymus (Figs. 9G & H).**

Megaspores with white ridges over a marguerite yellow to primrose yellow background, with or without a slightly developed equatorial flange; proximal face granulate or granulate-reticulate with open reticulum of low ridges, the microstructure irregularly micro-granulate; distal face reticulate with open reticulum of moderately high ridges, the microstructure smooth, with micro-foveolae; 215-240  $\mu\text{m}$  diam. Microspores tan, without an equatorial flange; proximal and distal faces with smooth, gemmate to clavate projections, the microstructure seemingly rugose; 25-30  $\mu\text{m}$  diam.

**3. *Selaginella simplex* Baker (Figs. 5E-H).**

Megaspores pinard yellow, frequently with an equatorial flange; proximal face granulose-tuberculate or rugulate, the microstructure micro-tubercled to micro-papillate, and micro-reticulate; distal face reticulate with open to close reticulum of low ridges, the microstructure densely micro-reticulate with rodlets, 260-300  $\mu\text{m}$  diam.

**4. *Selaginella correae* Valdespino (see Valdespino, 1993b: 317., Figs. 2A-D).**

Megaspores whitish, with or without a slightly developed equatorial flange; proximal face reticulate with close reticulum of low ridges, the microstructure with smooth, papilla-like projections, fusing to form ridges, micro-foveolate; distal face reticulate with open reticulum of rather low to medium ridges, the distal face

smooth, micro-foveolate; 230-260  $\mu\text{m}$  diam. Microspores tan to orange, without an equatorial flange; proximal and distal faces seemingly smooth, 25-40  $\mu\text{m}$  diam.

**5. *Selaginella hyalogramma* Valdespino (Figs. 6E-H).**

Megaspores pinard- to baryta yellow, with a prominent equatorial flange; proximal face reticulate with close reticulum of low ridges, the microstructure micro-echinulate to micro-papillate, with very obscure micro-foveolae; distal face reticulate with open reticulum of high ridges, the microstructure micro-echinulate to micro-papillate, with very obscure micro-foveolae; 270-300  $\mu\text{m}$  diam.

**6. *Selaginella muscosa* Spring (Figs. 6C & D; 9C & D).**

Megaspores baryta yellow to empire yellow or white, with a strongly developed equatorial flange (sometimes interrupted by perforations); proximal face seemingly smooth to granular, or striate marginally, the microstructure micro-echinulate; the distal face reticulate with open reticulum of high ridges, the microstructure micro-echinate and micro-foveolate; (280-)325-360  $\mu\text{m}$  diam. Microspores tan to orange, frequently with a weakly developed equatorial flange; proximal face centrally rugose, smoother near the margins, or seemingly smooth throughout; distal face clavate over a smooth microstructure, 18-30  $\mu\text{m}$  diam.

NOTE: The characterization of the spores presented here is in agreement with that submitted by Morbelli (1977) working with Argentinean populations of *S. muscosa*. Microspores examined of specimens from Trinidad and Tobago are

rather similar to those sampled from Brazil, although they tend to have shorter clavae (2-2.6  $\mu\text{m}$ ), whereas those from Brazil have longer clavae (5-7.3  $\mu\text{m}$ ). Morbelli's (1977) measurements of the clavae, however, encompass both ranges here described. The fact that microspores from Trinidad and Tobago do not have echinulate bacula, but smooth clavae supports a closer relationship with other populations of S. muscosa and argues against an alliance with S. tenella (see species description).

#### 7. *Selaginella porelloides* (Lamarck) Spring

Megaspores white, infrequently yellow, with a well developed equatorial flange; proximal face striate-reticulate to reticulate with open reticulum of high ridges, the microstructure micro-echinulate, with obscure to conspicuous micro-foveolae; distal face reticulate with open reticulum of high ridges, the microstructure micro-echinulate or with papilla-like projections covered with micro-echinae, and micro-foveolate; (230-)260-300(-350)  $\mu\text{m}$  diam. Microspores not seen.

#### 8. *Selaginella seemannii* Baker

Megaspores white, marguerite to massicot yellow (white to pale yellow), with a prominent equatorial flange; proximal face striate to reticulate with open reticulum of low ridges. the microstructure densely micro-cristate; distal face reticulate with open reticulum of high ridges, the microstructure micro-foveolate



and micro-papillate; 250-320  $\mu\text{m}$  diam.

**9. *Selaginella gynostachya* Valdespino**

Megaspores marguerite yellow (light yellow), with a well developed equatorial flange; proximal face striate-reticulate to reticulate with open reticulum of low ridges, the microstructure not observed; distal face reticulate with open reticulum of medium to high ridges, the microstructure not observed, 300-320  $\mu\text{m}$  diam.

**10. *Selaginella karowtipuensis* Valdespino**

Megaspores maize yellow, with a prominent equatorial flange; the proximal face striate-reticulate to reticulate with open reticulum of low ridges, the microstructure not observed; distal face reticulate with open reticulum of high ridges, the microstructure not observed; 320-340  $\mu\text{m}$  diam.

**11. *Selaginella lychnuchus* Spring**

Megaspores maize yellow, cream, pale yellow-orange, or pale orange-yellow, without an equatorial flange; the proximal face striate-reticulate with close to open reticulum of moderately high ridges, the microstructure rugose to micro-papillate, with micro-foveolae; distal face reticulate with open reticulum of rather high ridges, the microstructure rugose to slightly micro-papillate, with micro-foveolae; 240-290  $\mu\text{m}$  diam.

**12. *Selaginella ramosissima* Baker**

Megaspores cream to marguerite yellow (light-yellow), with an equatorial flange; the proximal face rugulate-reticulate to striate-reticulate with open to close reticulum of rather low ridges, microstructure micro-echinulate or slightly rugose to smooth, with micro-foveolae; distal face reticulate with open reticulum of high ridges, the microstructure micro-echinulate to smooth, with micro-foveolae, 220-235  $\mu\text{m}$  diam. Microspores tan to orange, without an equatorial flange; proximal face seemingly smooth, the microstructure not observed; distal face gemmate to verrucate, the microstructure not observed; 19-32  $\mu\text{m}$  diam.

**13. *Selaginella chionoloma* Alston ex Crabbe & Jermy**

Megaspores orange-buff, without an equatorial flange; proximal face rugulate or seemingly smooth, the microstructure densely micro-echinulate, with obscure micro-foveolae; distal face reticulate, with moderately high ridges, the microstructure micro-papillate to micro-echinulate, with micro-foveolae; 220-240  $\mu\text{m}$  diam. Microspores tan to orange, without an equatorial flange; proximal face seemingly smooth, the microstructure not observed; distal face verrucate to seemingly smooth, the microstructure not observed; 26-32  $\mu\text{m}$  diam.

**14. *Selaginella popayanensis* Hieronymus**

Megaspores orange-buff, light orange-yellow, or deep chrome (light orange to orange), frequently with a prominent equatorial flange; proximal face reticulate,

reticulate-striate, or corrugate-reticulate with open to close reticulum of moderately high ridges, the microstructure irregularly micro-granulate, micro-echinulate to micro-papillate, or smooth, with micro-foveolae; distal face reticulate or reticulate-corrugate with open reticulum of low and coarse or high ridges, the microstructure micro-foveolate; 240-295  $\mu\text{m}$  diam.

#### **15. *Selaginella moritziana* Spring**

Megaspores orange-buff, light orange-yellow, or deep chrome (light orange to orange), frequently with a prominent equatorial flange; proximal face reticulate-striate or corrugate-reticulate with open to close reticulum of moderately high ridges, the microstructure micro-papillate to micro-echinulate, with micro-foveolae; distal face reticulate or reticulate-corrugate with open reticulum of high ridges, microstructure micro-papillate to micro-echinulate, with micro-foveolae; 270-367  $\mu\text{m}$  diam.

NOTE: Megaspores of Steiermark 52967 from Ecuador differ from megaspores of other specimens examined in their larger size and in the sponge-like to micro-reticulate pattern of the microstructure on the distal face. They, however, are comparable to megaspores from other populations in their gross morphology.

#### **16. *Selaginella flacca* Alston**

Megaspores orange-buff, light orange-yellow, or deep chrome (light orange

to orange), without an equatorial flange; proximal face striate-corrugate to slightly striate-reticulate, with slightly developed close to open reticulum of low ridges, the microstructure micro-echinulate, with obscure micro-foveolae; distal face reticulate-rugose to reticulate, with open reticulum of low ridges, the microstructure rugose, with micro-foveolae; 250-280  $\mu\text{m}$  diam. Microspores light orange, without an equatorial flange; proximal and distal faces seemingly smooth, with micro-echinae, 19-20  $\mu\text{m}$  diam.

#### **17. *Selaginella cavifolia* A. Braun**

Megaspores capucine orange, pale yellow-orange, light orange-yellow, or orange-buff, usually without an equatorial flange or with a slightly developed one; proximal face striate-reticulate to reticulate, with close reticulum of rather low ridges, the microstructure micro-echinulate to micro-papillate, with micro-foveolae; distal face reticulate with open reticulum of high ridges, the microstructure rugose or micro-echinulate to micro-papillate, with micro-foveolate; 300-362  $\mu\text{m}$  diam.

#### **18. *Selaginella bernoullii* Hieronymus (Figs. 7F-J).**

Megaspores cream, usually without an equatorial flange or with a slightly developed one; proximal face rugulate to rugulate-reticulate with close reticulum of rather low ridges, the microstructure micro-echinulate and micro-foveolate; distal face reticulate with open reticulum of low ridges, the microstructure micro-foveolate and sparsely micro-echinulate to micro-papillate; 250-300  $\mu\text{m}$  diam.

**19. *Selaginella porphyrospora* A. Braun (Figs. 7A-E).**

Megaspores orange, with a well developed equatorial flange; proximal face reticulate to reticulate-rugulate with close reticulum of high, dense ridges, with central, papilla-like projections (apparently fusing to form the ridges), the microstructure micro-foveolate to rugose; distal face reticulate with open reticulum of high ridges, the microstructure micro-foveolate; 250-265  $\mu\text{m}$  diam.

**20. *Selaginella glossophylla* Alston ex Crabbe & Jermy**

Megaspores pale to light orange-yellow, without an equatorial flange; proximal face rugose to rugose-reticulate with close reticulum of rather low ridges, the microstructure with papilla-like projections covered with micro-papillae to micro-echinae or rugose and smooth, micro-foveolate; distal face reticulate with open reticulum of high ridges, the microstructure micro-papillate to smooth and micro-foveolate; 275-290  $\mu\text{m}$  diam.

NOTE: According to Crabbe and Jermy (1976) microspores are approximately 34  $\mu\text{m}$  diam.

**21. *Selaginella mixteca* Mickel & Beitel**

Megaspores pinard to baryta yellow (lemon-yellow), with or without an equatorial flange; proximal face seemingly striate-reticulate with close reticulum of low ridges, the microstructure not observed; distal face reticulate with close to open reticulum of low ridges, the microstructure not observed; 320-360  $\mu\text{m}$  diam.

**22. *Selaginella prolifera* Valdespino**

Megaspores snow-white, without an equatorial flange or with a slightly developed one; proximal face granulose-striate to granulose-reticulate with open reticulum of rather high ridges, the microstructure micro-granulate to micro-echinulate; distal face reticulate with open reticulum of low to high ridges, the microstructure micro-echinulate and micro-foveolate, 220-255  $\mu\text{m}$  diam.

**23. *Selaginella lineolata* Mickel & Beitel**

Megaspores bone-white, with a slightly to moderately developed equatorial flange; proximal face striate-reticulate with open reticulum of rather high ridges, the microstructure micro-echinulate, with micro-foveolae; distal face reticulate with open to close reticulum of low ridges, the microstructure micro-papillate to micro-echinulate, with micro-foveolae, 275-340  $\mu\text{m}$  diam.

**24. *Selaginella finitima* Mickel & Beitel**

Megaspores cream, with an equatorial flange; proximal face rugose, the microstructure not observed; distal face rugose-reticulate, with close reticulum of low ridges, the microstructure not observed, 150-250  $\mu\text{m}$  diam.

**25. *Selaginella tuberosa* McAlpin & Lellinger**

Megaspores not well observed, white to bone-white, seemingly without an equatorial flange; proximal face not readily observed; distal face reticulate with

seemingly close reticulum of low ridges, the microstructure not observed; not measured. Microspores immature.

**26. *Selaginella macilenta* Baker**

Megaspores snow-white, seemingly without an equatorial flange; proximal face seemingly smooth to rugulate, the microstructure not observed; distal face seemingly rugulate-reticulate with open reticulum of low ridges, the microstructure not observed; 240-260  $\mu\text{m}$  diam.

**27. *Selaginella flagellata* Spring (Figs. 9E & F).**

Megaspores snow-white, with an equatorial flange; proximal face rugose-granulate to granulate-reticulate, the microstructure micro-echinulate, with obscure micro-foveolae; distal face reticulate, with ridges of rather low to medium height, the microstructure micro-echinulate and micro-foveolate, with small micro-tubercles; 230-240  $\mu\text{m}$  diam. Microspores tan, with a weakly developed equatorial flange; the proximal face slightly rugose to smooth; distal face baculate to clavate over a rugose to seemingly smooth microstructure; 20-23  $\mu\text{m}$  diam.

NOTE: My observations of microspore morphology in this species are comparable to those of Hellwig (1969) in regard to size and sculpturing pattern. Roubik and Moreno (1991) characterized *S. flagellata* microspores as echinulate and with a wider equatorial diameter than the ones presented in the present study or that of Hellwig.

**28. *Selaginella stenophylla* A. Braun (see A Tryon & Lugardon, 1991: 617., Figs. 231.70 & 71).**

Megaspores white, infrequently cream to brownish, with a prominent equatorial flange; proximal face granular-striate, striate-reticulate, with close to open reticulum of low ridges, the microstructure with papilla-like projections covered by echinae, micro-echinulate, with micro-foveolae; distal face reticulate, with open reticulum of high ridges, the microstructure micro-echinulate and micro-foveolate; 330-356  $\mu\text{m}$  diam.

**29. *Selaginella tenella* (P. Beauv.) Spring (Figs. 8A-O; 9E & F).**

Megaspores snow-white to bone-white or yellowish with age, with or without an equatorial flange; proximal face granular, granular-rugose, or granular-reticulate marginally, with close reticula of low ridges, the microstructure micro-echinulate and with papilla-like projections covered with micro-echinae, with micro-foveolae; distal face reticulate, with close to open reticulum of low to high ridges, the microstructure micro-echinulate, micro-papillate, or micro-cristate, with obscure micro-foveolae; 230-270  $\mu\text{m}$  diam. Microspores tan to orange, without an equatorial flange; proximal face micro-echinulate; distal face baculate, over a micro-echinulate microstructure that extends into the bacula; 24-31  $\mu\text{m}$ .

**30. *Selaginella leucoloma* Alston ex Crabbe & Jermy**

Megaspores straw, baryta, or naphthalene yellow (light lemon-yellow),



without an equatorial flange; proximal face seemingly smooth or granulose near laesura, rugulate-striate marginally, the microstructure micro-papillate to micro-echinulate, micro-foveolate, and frequently with micro-echinulate granules; distal face reticulate with close reticulum of low ridges, the microstructure micro-granulate, micro-papillate to micro-echinulate, and micro-foveolate; 210-235  $\mu\text{m}$  diam.

NOTE: According to Crabbe and Jermy (1976), microspores are approximately 37.5  $\mu\text{m}$  diam.

### **31. *Selaginella sobolifera* A. R. Smith**

Megaspores massicot to naphthalene yellow, with or without an equatorial flange, the proximal face striate-rugulate to seemingly smooth, the distal face reticulate with open reticulum of moderately high ridges; 220-255  $\mu\text{m}$  diam.

Microspores tan to orange, without an equatorial flange; proximal and distal faces clavate, the microstructure not observed, 24-39  $\mu\text{m}$  diam.

Figure 5. SEM micrographs of Selaginella megaspores. A-D. S. minima (Johnston 878, NY). A. Proximal face. B. Detail of proximal face. C. Distal face. D. Detail of distal face. E-H. S. simplex (Valdespino 1290, NY). E. Proximal face. F. Detail proximal face. G. Distal face. H. Detail of distal face. (Scale bar: A, C, E, and G = 100  $\mu\text{m}$ ; B, D, F, and H = 10  $\mu\text{m}$ .). Alston et al. (1981) doubted the distinctness of these two species, however, besides other differences in vegetative morphological characteristics (Valdespino, 1993b) they are easy to distinguish by their spore morphology.

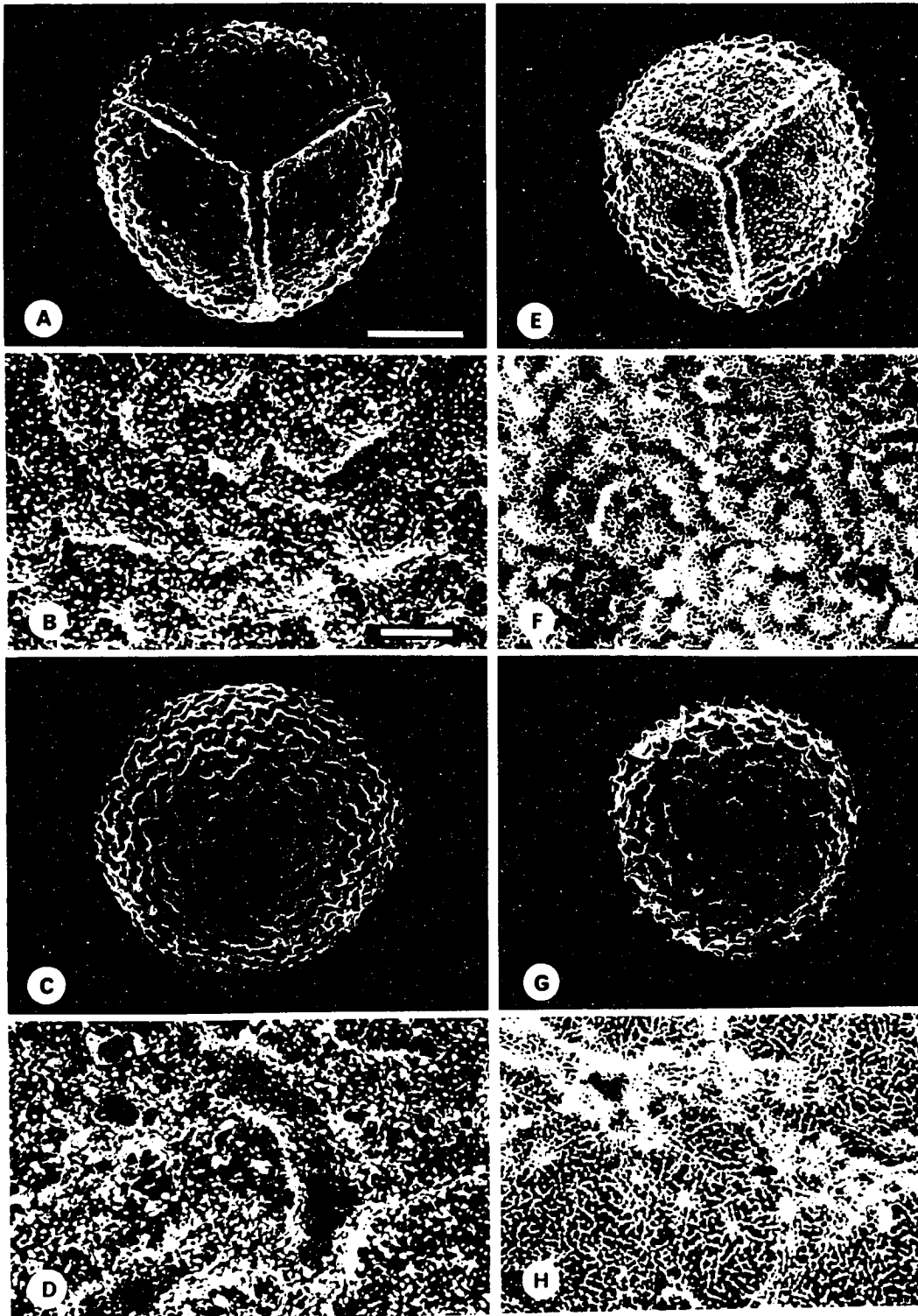


Figure 6. SEM micrographs of Selaginella megaspores. A-D. S. muscosa (Rose & Russell 20441, NY). A. Proximal face; note equatorial flange. B. Detail of proximal face. C. Distal face. D. Detail of distal face. E-H. S. hyalogramma. (Davidse & González 21525, MO). E. Proximal face; note equatorial flange and reticulate sculpturing pattern. F. Detail of proximal face. G. Distal face. H. Detail of distal face. (Scale bar: A, C, E & G = 100  $\mu\text{m}$ ; B, D, F & H = 10  $\mu\text{m}$ ).

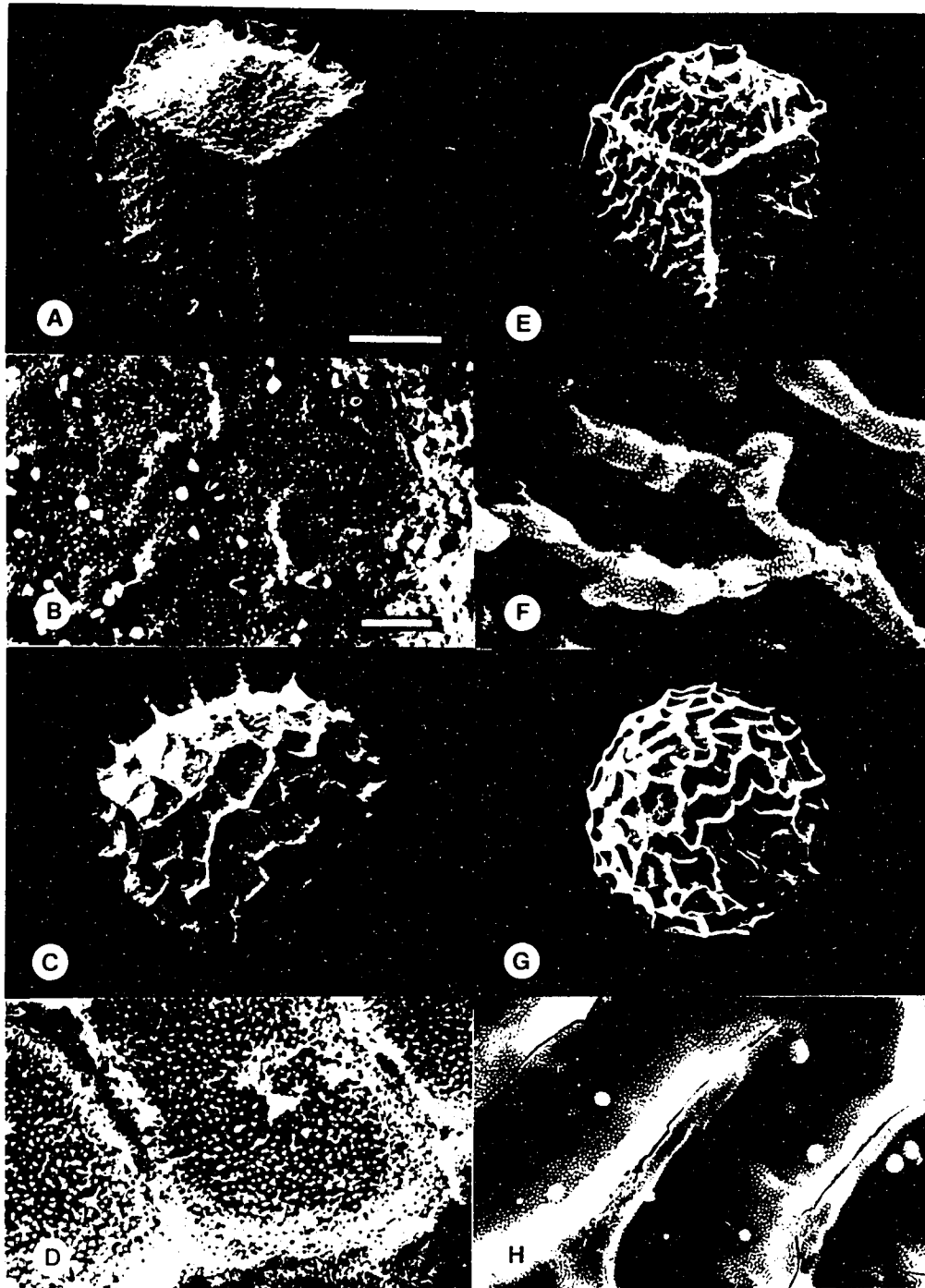


Figure 7. SEM micrographs of Selaginella megaspores. A-E. S. porphyrospora (Valdespino 1269, NY). A. Proximal face. B & C. Detail of proximal face. D. Distal face. E. Detail of distal face. F-J. S. bernoullii (Mickel 5092, NY). F. Proximal face; note absence of equatorial flange. G & H. Detail of proximal face. I. Distal face. J. Detail of distal face. (Scale bar: A, D, F & I = 100  $\mu\text{m}$ ; B, E, G & J = 10  $\mu\text{m}$ ; C & H = 5  $\mu\text{m}$ ).

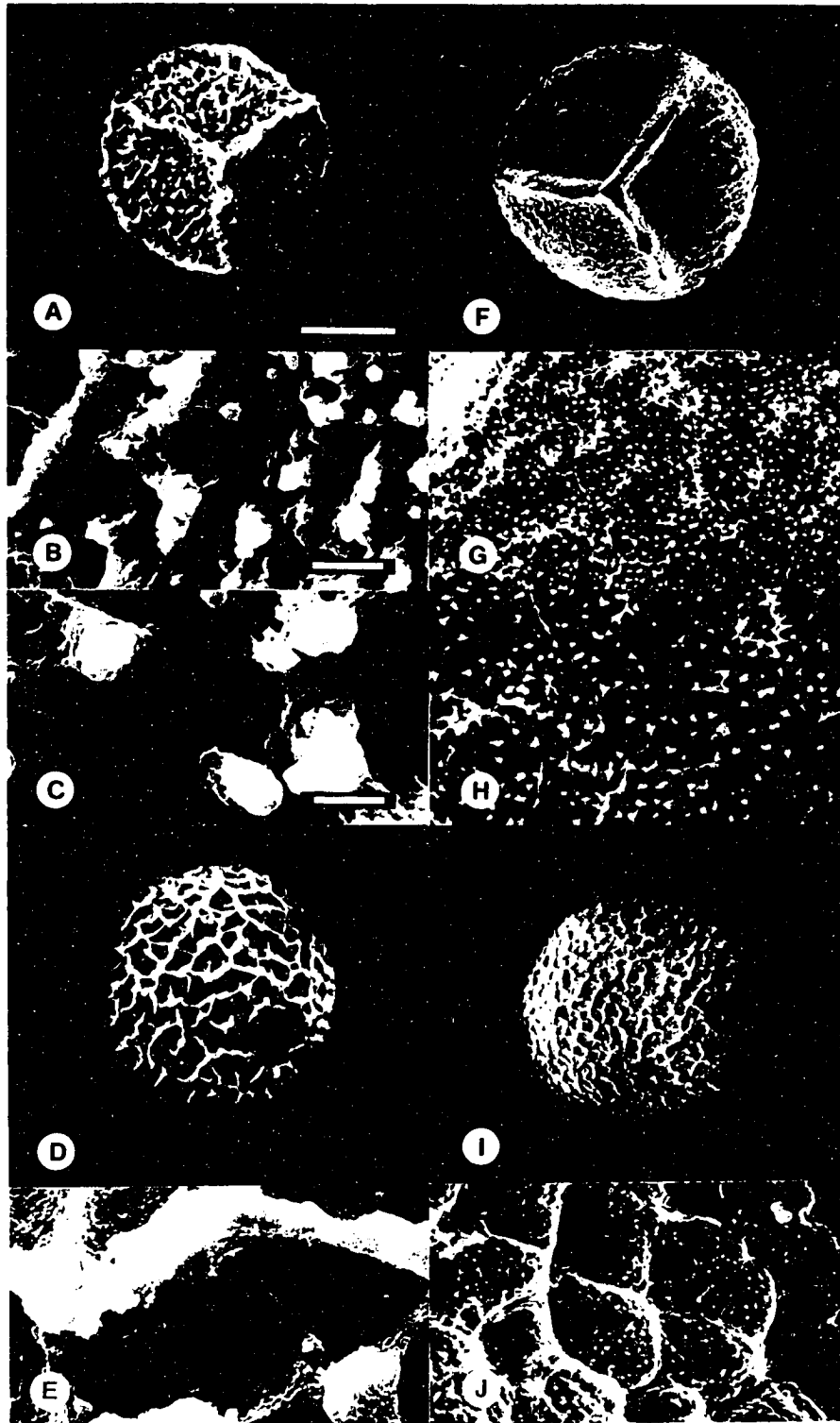


Figure 8. SEM micrographs of megaspores of the Selaginella tenella complex from different populations. A-E. (Puerto Rico, Britton 8623, NY). A. Proximal face. B. Detail of proximal face. C. Distal face. D & E. Detail of distal face. F-J. (Puerto Rico, Grimes et al. 3217, NY). F. Proximal face. G. Detail of proximal face. H. Distal face. I & J. Detail of distal face. K-O. (Panama, Valdespino et al. 1367, NY). K. Proximal face. L. Detail of proximal face. M. Distal face. N & O. Detail of distal face. (Scale bar: A, C, F, H, K, and M = 100  $\mu\text{m}$ ; B, E, G, J, L, and O = 5  $\mu\text{m}$ ; D, I, and N = 10  $\mu\text{m}$ .).



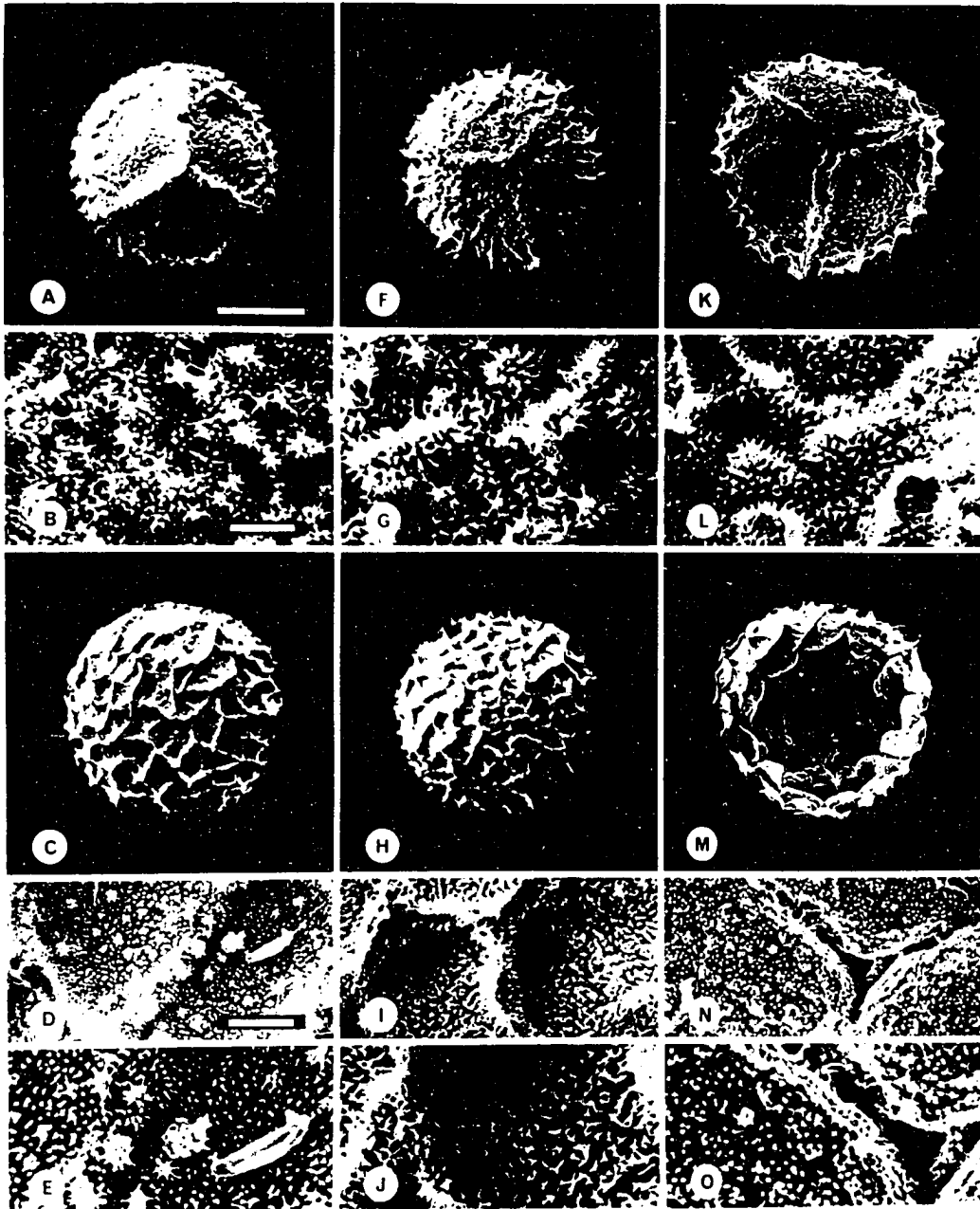
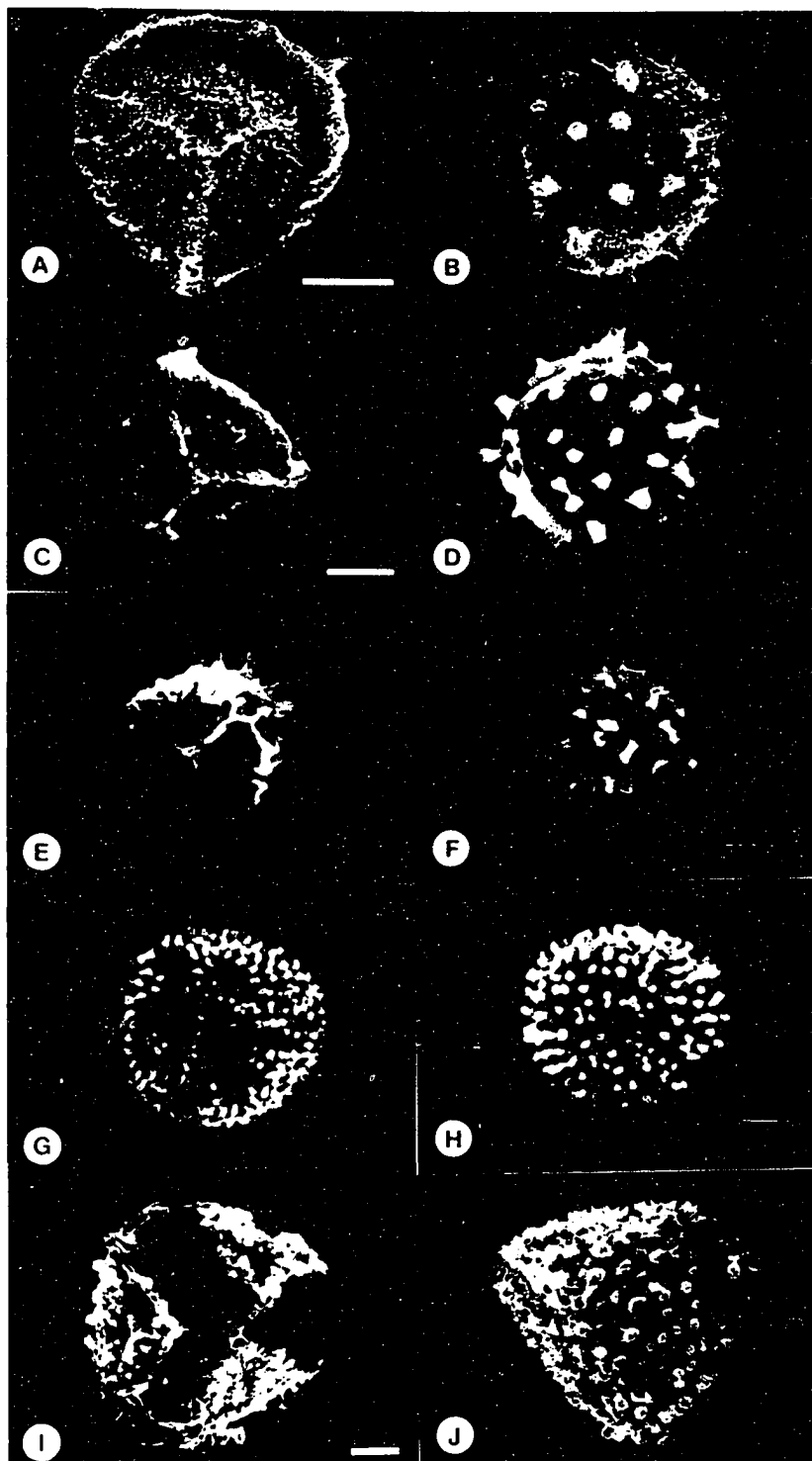


Figure 9. SEM micrographs of Selaginella microspores. A & B. S. tenella (Valdespino 1367, NY). A. Proximal face. B. Distal face. C & D. S. muscosa (R. Tryon & A. Tryon 6654, GH). C. Proximal face. D. Distal face; note incipient equatorial flange. E & F. S. flagellata (Ll. Williams & Alston 205, AAU). E. Proximal face. F. Distal face. G & H. S. broadwayi (Broadway 5196, MO). G. Proximal face. H. Distal face. I & J. S. minima (Peña & R. Foster 210, F). I. Proximal face. J. Distal face. (Scale bar: A & B = 10  $\mu\text{m}$ ; C, D, E, F, G & H = 10  $\mu\text{m}$ ; I & J. = 10  $\mu\text{m}$ ).



## CHAPTER -VI

### PHYTOCHEMICAL STUDIES

#### VI.1. FLAVONOID STUDIES IN *SELAGINELLA*

##### VI.1.1. INTRODUCTION

The study of the composition and distribution of plant secondary metabolites is considered most useful in systematic and plant evolutionary studies (Cooper-Driver & Haufler, 1983). Among this class of compounds the flavonoids and related phenolic compounds have proved to be a reliable data source in the determination and understanding of phylogenetic relationships within different plant groups (Cooper-Driver, 1980; Cooper-Driver & Haufler, 1983; Geiger & Quinn, 1988; Harborne, 1977).

The usefulness of flavonoids in pteridophytes has been significant, particularly in determining phylogenetic relationships at the infraspecific (Smith, 1980), interspecific (Smith & Levin, 1963), generic (Giannasi, 1980; Giannasi & Mickel, 1979), and higher (Umikalsom et al., 1994; Voirin, 1972; Voirin & Jay, 1978; Wallace et al., 1983) taxonomic levels.

Phytochemical studies in Selaginella have reported the presence of several secondary compounds in this genus, in particular phenol conjugates, simple flavones, and biflavones (Chakravarthy et al., 1981; Lin et al., 1987, 1994; López-Sáez et al., 1994a; Okigawa et al., 1971; Qasim et al., 1985; Somers, 1978; Voirin, 1972; Voirin & Jay, 1978; White & Towers, 1967). A useful summary of most of

these studies and of the species of Selaginella previously analyzed is provided by López-Sáez et al. (1994b).

According to the majority of these studies the genus Selaginella is characterized by the presence of biflavones, particularly amentoflavone, hinokiflavone and their methyl ethers (Markham, 1988). Interestingly, and as pointed out by Richardson (1989), the first flavonoid study in Selaginella, conducted by Harada and Saiki (1955), reported the presence of the simple flavone apigenin. Somers (1978), studying 16 species classified in series Articulatae Spring, found only mono- and di-C-glycosylflavones of apigenin and luteolin. According to these two studies, it appears that some simple flavones and their C-glycosyl derivatives are also present in Selaginella. The discrepancy in results relating to the nature of flavonoids present in Selaginella will be addressed in the Results and Discussion section.

There are few previous attempts to correlate flavonoid data with existing classifications of Selaginella (i.e., Somers, 1978) and with presumably related lycopod taxa (i.e., Voirin, 1972; Voirin & Jay, 1978), but the limited number of species sampled has hampered meaningful conclusions, and thus generalizations for the whole genus could not be made. Nevertheless, Somers' study suggested that the presence and distribution patterns of flavonoids, particularly of luteolin-type compounds among the studied species, have taxonomic significance.

## VI.2. INVESTIGATION OF FLAVONOIDS IN SELAGINELLA WITH EMPHASIS ON SUBG.

***HETEROSTACHYS***

The genus Selaginella contains about 700 species, of which about only 40 species or about 6% of them have been phytochemically studied before the present study.

As a part of my dissertation research on Selaginella subg. Heterostachys in Central and South America, a preliminary analysis of flavonoids present in several species of Selaginella, with emphasis on those classified within subg. Heterostachys, was made in collaboration with Dr. B. Meurer-Grimes (Lehman College-City University of New York and NYBG).

**VI.2.1. OBJECTIVES**

The objectives of this study were to:

A. Study the composition and distribution of flavonoids in selected species of Selaginella representing most of the subgenera proposed by Jermy (1986, 1990), with emphasis on those species within subg. Heterostachys.

B. Determine if the flavonoid composition of the different species studied can provide additional and independent data to help define subg. Heterostachys and to determine phylogenetic relationships among the subgenera proposed by Jermy.

**VI.2.2. MATERIALS AND METHODS**

I collected living plants as well as dried samples during field work in

Panama, Costa Rica, Ecuador, and Brazil (Fig. 1E). Living specimens were kept under cultivation at the Propagation Center of The New York Botanical Garden (Fig. 1F). This living material served as the source of fresh material for most of the phytochemical studies. Additionally, living plants of S. rupestris (L.) Spring from North Carolina, dried material of S. diffusa (C. Presl) from Bolivia, S. laxifolia Baker and S. substipitata Spring from Puerto Rico, and S. selaginoides (L.) P. Beauv. ex Schrank & Martius from Switzerland, and a crude extract of S. denticulata (L.) Spring from Spain were generously provided by Mr. William Moye, Dr. Michael Nee, M.Sc. Carlos Sánchez, Mr. Beat Fischer, and Dr. J. A. López-Sáez, respectively.

The methodology followed here for flavonoid analysis has been outlined in detail by Meurer-Grimes and Stevenson (1994), and thus it is only summarized here.

#### VI.2.3. EXTRACTIONS FOR FLAVONOIDS ANALYSIS IN CRUDE EXTRACTS

Leaf material corresponding to 0.1-0.5 g fresh or dried weight were homogenized with a Polytron homogenizer in 5-15 ml of 80% aq. MeOH. The crude extracts were then extracted under stirring for 1 hr at room temperature and centrifuged for 5 min., the supernatant was collected and transferred to a vial, and the pellet was extracted a second time with 5 ml of 80% aq. MeOH under the same conditions. The combined extracts were stored at -20°C until further analysis.

#### VI.2.4. HPLC-ANALYSIS OF BIFLAVONES IN CRUDE EXTRACTS

Separation of the 80% aq. methanolic crude extracts of Selaginella were obtained by analytical HPLC on a Nucleosil C-18 column (4.6 mm × 250 mm i.d., 5  $\mu$ , Macherey & Nagel, Düren, Germany) at a flow rate of 1 ml min<sup>-1</sup> using a linear gradient: 0 min: 60% solvent A in B, 30 min: 30% solvent A in B, 34 min: 30% solvent A in B; solvent A: 1% H<sub>3</sub>PO<sub>4</sub> in H<sub>2</sub>O; solvent B: MeCN. The injection volume was 50  $\mu$ l. All separations were monitored with a photodiode array detector at 220-440 nm.

The biflavones were characterized by their retention times relative to hinokiflavone [ $RR_t = R_t \text{ (other biflavonoids)} \div R_t \text{ (hinokiflavone)}$ ].

The biflavones were identified by co-chromatography with internal standards of authentic biflavones using HPLC- and TLC-analysis. The internal standards amentoflavone, bilobetin, ginkgetin, isoginkgetin, and hinokiflavone became available through the phytochemical study on the flavonoids in the Cycadales by Meurer-Grimes and Stevenson (1994). They used plant material of Ginkgo biloba L. and Dioon spinulosum Dyer as a source for the isolation of the internal biflavone standards. The procedure for the extraction and purification of internal standards is described in Meurer-Grimes and Stevenson (1994). Additional standards of amentoflavone, robustaflavone, hinokiflavone, isocryptomerin, and cryptomerin B were generously provided by Dr. López-Sáez (see López-Sáez et al., 1994a, b).



#### VI.2.5. TLC-ANALYSIS

Crude extracts were separated on silica gel plates (F-254) using toluene-EtOAc-HCOOH (5:4:1) as a solvent. The plates were developed twice, and evaluated under UV-light at 254 and 366 nm.

#### VI.2.6. ISOLATION AND PURIFICATION OF BIFLAVONES FROM *S. WILLDENOWII*

Leaf material corresponding to 287.2 g fresh weight of *S. willdenowii* was homogenized in a commercial blender, and extracted twice for 1 hr under stirring at room temperature with a total of 3 liters of 80% aq. MeOH. The combined crude extracts were then evaporated to a syrupy consistency and poured on top of 100 g of Polyamide CC-6 (Machery & Nagel, Düren, Germany) that had been presoaked in water. A small amount of the syrupy extract was retained for analytical HPLC. The crude extract was eluted under vacuum with 1 l each of H<sub>2</sub>O, 40% aq. MeOH, (2×) 80% aq. MeOH, and Abs. MeOH. All fractions were then evaporated, diluted in a small volume of 80% aq. MeOH, and analyzed by the analytical method described above. Few biflavones were present in the methanolic fractions. The biflavones were mostly present in the water fraction, which was mixed with 1 l of EtOAc and partitioned in a separatory funnel. The resulting EtOAc fraction was then evaporated and analyzed by analytical HPLC. It contained a large concentration of all the biflavones found in the original crude extract. The biflavones from the EtOAc fraction were then separated by preparative HPLC using a Waters Bondapak TM/C-18 column (30 cm × 1 cm i.d.,

5  $\mu$ ) at a flow rate of 3.5 ml/min with on-line UV-detection from 220 to 400 nm. The biflavone fractions resulting from the preparative HPLC-analysis yielded 5 pure biflavones as determined by analytical HPLC. These biflavones will be sent to Spain, where Dr. López-Sáez will analyze them by  $^1\text{H}$  NMR spectroscopy to determine their precise chemical structure.

#### VI.2.7. RESULTS AND DISCUSSION

Thirty-nine samples representing 27 selected taxa of homophyllous and heterophyllous selaginellas classified in subgenera Selaginella, Tetragonostachys, Stachygynandrum (including species of series Articulatae), and Heterostachys, were surveyed (Table II). This study was the first in which HPLC was applied for flavonoid analysis of Selaginella species.

Several biflavones were detected by HPLC-analysis of the crude extracts from the species surveyed. A total of six of these were identified by co-chromatography with the internal standards mentioned above. Other biflavones await further identification and characterization by co-chromatography, NMR- and MS-spectroscopy. The results showing the distribution of biflavones are presented in Table II. An average of the relative retention times ( $\text{RR}_t$ ) of the biflavones as well as their UV-absorption spectra, TLC  $R_f$ -values, and color reactions are presented in Table III. An example of a representative HPLC-analysis of the biflavones in crude extracts is shown in Fig. 10. Only the biflavones identified by co-chromatography (Fig. 11) and some other unknown, but taxonomically useful

biflavones are listed.

In this study, it was observed that biflavonoid breakdown with drying and prolonged storage at +4°C may occur. In some cases there were some quantitative and qualitative differences in the flavonoid profiles obtained by HPLC-analysis of fresh and dried samples from the same plant or species. Most noticeable, after drying fresh material of S. galeottii, an increase in the amount of robustaflavone accompanied by a decrease in the amount of amentoflavone was detected. This may be due to intramolecular rearrangement. It was concluded that drying of the plant material can introduce artifacts. Similar changes in the concentration of flavonoids in fresh and dried plant material were observed by Iwashina et al. (1993). They noted that in some flavonoid profiles obtained from species of the fern genus Cheilanthes some compounds were absent from dried samples but present in fresh samples. In our study an effort was made to use fresh material as much as possible, but for some species only dried material was available. These results should be interpreted with caution.

Examination of different population samples of the same species within subg. Heterostachys revealed no differences in biflavone composition between different populations; they all had the same biflavone profile. Among these species, examination of the biflavone profile of S. moritziana from two different populations reveals that this species seems to be characterized by the presence of only amentoflavone and hinokiflavone with only traces of robustaflavone, whereas most of the other species studied definitively had robustaflavone as a major

constituent.

Our results indicate that Selaginella is characterized by the presence of amentoflavone and hinokiflavone (Markham, 1988), as well as of robustaflavone. Robustaflavone, which was previously identified from only two other species of Selaginella (Qasim et al., 1985; López-Sáez et al., 1994b), is rather common among the studied species (see Table II). According to López-Sáez et al. (1994b), the occurrence of hinokiflavone in Selaginella is sporadic; however, our results clearly indicate that it was present in all species investigated.

The three species of series Articulatae (articulate group) analyzed here (see Table II) were also studied previously. Selaginella galeottii was studied as S. stellata Spring by Somers (1978) using PC and UV-spectral analysis. He reported mostly luteolin type derivatives (i.e., mono- and di-C-glycosylflavones) from these species (see Somers, 1978, Table XII). He did not observe any biflavones. His results are very puzzling because they are only the second and most recent report of simple flavones in Selaginella, and our results contradict his findings. In fact, our data show that these three articulate species were among the most diverse in terms of the number of biflavones detected by HPLC-analysis (see Table II). Our analysis failed to confirm the presence of any simple flavones in them.

Interestingly, in Somers' study of the articulate species S. kraussiana (Kunze) A. Braun, no simple flavones or biflavones were detected. In his view, the lack of any flavones in this species was certainly not a surprise, but a confirmation of the somewhat uncertain position of S. kraussiana in relation to the

other articulate species. He pointed out that his phytochemical data for this species were in agreement with certain morphological characteristics and the distribution pattern that set this species apart from other species of series Articulatae. Independent study by Qasim et al. (1985) and a preliminary analysis by Meurer-Grimes (unpublished) of S. kraussiana are in disagreement with Somers' results and clearly show that this species is also characterized by the presence of biflavones. Qasim et al. (1985) isolated amentoflavone, hinokiflavone, and isocryptomerin from it. In Meurer-Grimes' preliminary analysis, she confirmed the occurrence of at least three major biflavones and some minor biflavones. Therefore, the flavonoid profile of S. kraussiana is similar to other articulate species.

In general, it is possible that Somers' report of simple flavones in Selaginella as well as the report of Harada and Saiki (1955) may be due to the relative inaccuracy of the techniques employed to isolate and identify the flavonoids. It should be pointed out that these initial phytochemical studies on the flavonoids of Selaginella were conducted using mostly paper chromatography (PC), thin-layer chromatography (TLC), and UV-spectral analysis. More advanced phytochemical techniques such as high performance liquid chromatography (HPLC), which provides high resolution of even structurally related flavonoids, were not applied. The techniques employed by Somers (1978) and Harada and Saiki (1955) are no longer considered accurate when used alone for detection and identification of a specific flavonoid (Geiger & Quinn, 1988). Biflavones are

known to have many physical and chemical properties similar to those of their component monomers (i.e., simple flavones) that makes them difficult to recognize by e.g., UV-spectral analysis, color tests, etc. (Markham, 1982). An alternative explanation for Somers' finding is that throughout his study he used field-dried specimens and we now know from our study that there may be degradation of biflavones in drying. Perhaps biflavones were present in the species studied by him and underwent degradation, presumably after a long storage period, to their respective monomers that were then detected in his analysis.

Most recent studies of flavonoids in Selaginella lend support for the presence of only biflavones in the genus (Lin et al., 1994; López-Sáez et al. 1994a, 1994b). Our data are also in agreement with their findings and confirm that biflavones are characteristic of the Selaginellaceae.

Another interesting finding of our study in relation to the species of series Articulatae is that S. galeottii and S. exaltata share an unknown biflavone ( $X_c$ ), not listed on Table II, with a  $RR_t = 1.4-1.44$  min (in S. diffusa  $RR_t = 1.38$  min). This biflavone was also found in three non-articulate species, S. braunii, S. willdenowii, and S. plana, a group here referred to as "the S. willdenowii group." These three species are similar to species in the articulate group in frequently having a reddish stem, some of the largest megaspores in the genus, frequently echinate and beige microspores, and usually a complex stelar pattern. In fact, S. willdenowii has several characteristics (e.g., a very similar habit, general morphology, complex stelar pattern, frequently dorsal rhizophores, a reduced number of megasporangia

that are protected by a larger megasporophyll, and large, white to bone-white megaspores with stout echinate to -baculate projections on the proximal and distal face, which fuse together on the distal face to form high ridges) that resemble those of S. exaltata and S. gigantea Steyermark & A. R. Smith of the series Articulatae. The presence of the unknown biflavone supports an alliance, based on morphological characteristics, between species in series Articulatae and species in the S. willdenowii group. If such alliance does exist, it is possible that the articulate group of selaginellas, characterized by a stem with mostly more than one meristele, may have arisen from or have a common ancestor with species in the S. willdenowii group.

The biflavone data of the species of the subg. Heterostachys analyzed here show that their flavonoid composition is similar to that of other heterophyllous Selaginella species (i.e., subg. Stachygynandrum) and of the homophyllous species (i.e., subg. Selaginella, subg. Tetragonostachys) investigated, and that no single biflavone character seems to set them apart (see Table II). Their biflavone profile suggests a rather close relationship between them and the other heterophyllous species.

The presence of a biflavone with an av.  $RR_t = 0.85$  min and UV-absorption maxima of 267 and 334 nm, identified as bilobetin by co-chromatography, seems to characterize all populations of S. porphyrospora and S. tenella studied. The same biflavone was also found in heterophyllous species not classified within subg. Heterostachys including S. diffusa of series Articulatae, S. willdenowii and S. plana

of the S. willdenowii group, and S. hoffmannii (see Tables II & III). Similarly, another unknown biflavone  $X_c$  with an av.  $RR_t = 0.92$  min and a UV-absorption maxima of 268 and 336 nm, was found in two of the species classified in subg. Heterostachys (S. muscosa and S. seemannii), species of series Articulatae, of the S. willdenowii group, and S. hoffmannii. Interestingly, the latter two species groups and S. hoffmannii are usually characterized by having red stems. Selaginella porphyrospora, S. tenella, S. muscosa, and S. seemannii have straw-colored or green stems. The fact that some species in subg. Heterostachys uniquely share some biflavones (bilobetin and  $X_c$ ) with red-stemmed species seems to indicate a relationship between species classified in subg. Heterostachys and those belonging to the S. willdenowii group and to subg. Stachygynandrum series Articulatae. Before we can generalize our findings, it will be desirable to study phytochemically other species of subg. Heterostachys, particularly from the Old World, where approximately two-thirds of the species in this subgenus are found.

The distribution pattern of biflavones in homophyllous species of subg. Tetragonostachys was similar to all the other taxa surveyed in that they have amentoflavone, robustaflavone, and hinokiflavone as major biflavones, but they also consistently show the presence of isocryptomerin as a major biflavone (Table II). Isocryptomerin also occurs sporadically in heterophyllous species. This flavonoid character supports a strong alliance among the members of subg. Tetragonostachys surveyed, but surprisingly does not argue in favor of a separate lineage from the heterophyllous species. This is most interesting because there is



a wealth of morphological data (Jermy, 1990; Mukhopadhyay & Sen, 1986; Valdespino, 1993a) that seems to support the inclusion of all members of subg. Tetragonostachys in a separate genus, which in fact has been already proposed by Soják (1992).

To my knowledge, the only previous study of biflavones in species of subg. Tetragonostachys was conducted by Chakravarthy et al. (1981). They reported the isolation of amentoflavone from material of S. rupestris collected in India. I believe it is very doubtful, however, that they actually studied this species, because S. rupestris is native to North America (Valdespino, 1993a); it does not occur naturally in India, and to our knowledge is not widely cultivated. They probably studied another member of subg. Tetragonostachys, most likely S. indica (Milde) Tryon or S. wightii Hieron. var. wightii, both of which are native to India (Tryon, 1955).

In this context, we should also mention that a similar case of mistaken identity may be responsible for the report of several biflavones obtained from plant material of S. lepidophylla (Hook. & Grev.) Spring collected in the Jaipur region of India by Qasim et al. (1985). Selaginella lepidophylla is not native to India, but to the states of New Mexico and Texas in the U.S.A. and of Mexico (Valdespino, 1993a), and it is unlikely that they actually studied this species. It is more probable that they studied S. tamariscina (P. Beauv.) Spring [S. pulvinata (Hook. & Grev.) Maxim. of Dixit, 1992], which is very similar in habit to S. lepidophylla, and is native to India. If in fact Qasim et al. (1985) did study S.

tamariscina, then we may expect that other independent phytochemical studies of the same species would have uncovered the same or most of the biflavones reported by Qasim et al. The López-Sáez et al. (1994b) summary of previous biflavones studies in S. tamariscina confirms the presence of all major biflavones isolated by Qasim et al. (1985) in this species. These studies also reported cryptomerin B in S. tamariscina, which apparently was not isolated or detected by Qasim et al. Some of the other biflavones, robustaflavone, di- and trimethylether of hinokiflavone, and heveaflavone, reported in Qasim et al. (1985) have not been confirmed by other studies.

Of the two species currently classified in the homophyllous subg. Selaginella, which traditionally has been regarded as the least derived subgenus (but see comments in Valdespino, 1993a), we were able to secure a sample of S. selaginoides from Switzerland. Our HPLC-analysis confirmed the presence of amentoflavone, robustaflavone, and hinokiflavone as previously reported by López-Sáez et al (1994a). In addition to those biflavones, we were able to detect traces of two minor biflavones with  $RR_t = 0.81$  min, UV-absorption maxima of 268 and 319 nm, and with  $RR_t = 0.27$  min, UV-absorption maxima of 267 and 336 nm, respectively. Contrary to a simple scenario that may have been expected according to the traditional phylogenetic view of S. selaginoides, we found that already there are all three amentoflavone, hinokiflavone, and robustaflavone type biflavones present in this species. This seems to indicate that, at least phytochemically, S. selaginoides is not far removed from other homophyllous and heterophyllous

species of the genus, and its flavonoid composition does not indicate any ancestral condition.

The HPLC-analysis of the crude extract of S. denticulata obtained from Spain confirmed the presence of amentoflavone, robustaflavone, hinokiflavone, isocryptomerin, and cryptomerin B (although only traces) in this species as reported by López-Sáez et al (1994b). We, could not confirm, however, the occurrence of the tetramethylether of amentoflavone and sotetsuflavone as reported by López-Sáez (1994b).

Table II  
DISTRIBUTION OF BIFLAVONES IN *SELAGINELLA* SPECIES<sup>1</sup>

| Species <sup>2</sup>                                          | Source <sup>3</sup> | A <sup>4</sup> | R   | B | H | IC | C | X <sub>a</sub> | X <sub>b</sub> | X <sub>c</sub> | X <sub>d</sub> |
|---------------------------------------------------------------|---------------------|----------------|-----|---|---|----|---|----------------|----------------|----------------|----------------|
| subg. Selaginella                                             |                     |                |     |   |   |    |   |                |                |                |                |
| <i>S. selaginoides</i> (L.) P. Beauv.<br>ex Martius & Schrank | BF1                 | + <sup>5</sup> | +   | - | + | -  | - | -              | +              | -              | -              |
| subg. Tetragonostachys                                        |                     |                |     |   |   |    |   |                |                |                |                |
| <i>S. arizonica</i> Maxon                                     | 1397                | +              | +   | - | + | +  | - | -              | -              | -              | -              |
| <i>S. basipilosa</i> Valdespino                               | 1396                | +              | +   | - | + | +  | - | -              | -              | -              | -              |
| <i>S. peruviana</i> (Milde) Hieron.                           | 1395                | +              | +   | - | + | +  | - | -              | -              | -              | -              |
| <i>S. rupestris</i> (L.) Spring                               | PS1                 | (+)            | (+) | - | + | +  | - | -              | -              | -              | -              |
| <i>S. underwoodii</i> Hieron.                                 | 1398                | +              | +   | - | + | +  | - | -              | -              | -              | -              |
| subg. Stachygynandrum                                         |                     |                |     |   |   |    |   |                |                |                |                |
| <i>S. acanthostachys</i> Baker                                | 1087                | +              | (+) | - | + | -  | - | -              | -              | -              | -              |
| <i>S. braunii</i> Baker                                       | PS5                 | +              | +   | - | + | -  | - | -              | +              | -              | -              |
| <i>S. denticulata</i> (L.) Spring                             | L1                  | +              | +   | - | + | +  | - | -              | -              | -              | -              |
| <i>S. estrellensis</i> Hieron.                                | 1266                | +              | +   | - | + | -  | - | -              | -              | -              | -              |
| <i>S. hoffmannii</i> Hieron.                                  | 1383                | +              | +   | - | + | +  | - | -              | +              | +              | -              |
| <i>S. jungermannioides</i> (Gaud.) Spring                     | 1379                | +              | +   | - | + | +  | + | -              | -              | -              | -              |
| <i>S. jungermannioides</i> (Gaud.) Spring                     | 1382                | +              | +   | - | ? | ?  | + | -              | -              | -              | -              |

Table II (continued)

| Species <sup>2</sup>                 | Source <sup>3</sup> | A <sup>4</sup> | R   | B | H | IC | C | X <sub>a</sub> | X <sub>b</sub> | X <sub>c</sub> | X <sub>d</sub> |
|--------------------------------------|---------------------|----------------|-----|---|---|----|---|----------------|----------------|----------------|----------------|
| <i>S. martensii</i> Spring           | 1276                | + <sup>5</sup> | ?   | ? | ? | ?  | - | -              | -              | -              | -              |
| <i>S. martensii</i> Spring           | 1279                | +              | ?   | ? | ? | ?  | - | -              | -              | -              | -              |
| <i>S. nipponica</i> Franch. & Savat. | PS6                 | +              | +   | - | + | -  | - | -              | -              | -              | -              |
| <i>S. plana</i> (Desv.) Hieron.      | NY 2f.              | +              | +   | + | + | -  | - | -              | -              | +              | +              |
| <i>S. plana</i> (Desv.) Hieron.      | NY 2d.              | +              | +   | + | + | -  | - | -              | -              | +              | -              |
| <i>S. plana</i> (Desv.) Hieron.      | PS4                 | +              | +   | - | + | +  | - | +              | +              | +              | +              |
| <i>S. substipitata</i> Spring        | S97                 | +              | (+) | - | + | +  | - | -              | -              | -              | -              |
| <i>S. wilddenowii</i> (Desv.) Baker  | NY 3f.              | +              | +   | + | + | -  | - | -              | -              | +              | -              |
| <i>S. wilddenowii</i> (Desv.) Baker  | NY 3d.              | +              | +   | + | + | -  | - | -              | -              | +              | -              |
| <i>S. wilddenowii</i> (Desv.) Baker  | PS3                 | +              | +   | - | + | +  | - | +              | +              | +              | +              |
| series Articulatae                   |                     |                |     |   |   |    |   |                |                |                |                |
| <i>S. diffusa</i> (C. Presl) Spring  | N45/134             | +              | +   | - | + | +  | + | -              | +              | +              | -              |
| <i>S. exaltata</i> (Kunze) Spring    | 1355                | +              | +   | + | + | -  | - | -              | -              | +              | -              |
| <i>S. galeottii</i> Spring           | 1280                | +              | +   | - | + | -  | - | -              | -              | -              | -              |
| <i>S. galeottii</i> Spring           | NY 1f.              | +              | +   | + | + | -  | - | -              | -              | +              | +              |
| <i>S. galeottii</i> Spring           | NY 1d.              | +              | +   | + | + | -  | - | -              | -              | +              | -              |
| subg. Heterostachys                  |                     |                |     |   |   |    |   |                |                |                |                |
| <i>S. laxifolia</i> Baker            | S16                 | ?              | ?   | - | + | -  | - | -              | -              | -              | -              |

Table II (continued)

| Species <sup>2</sup>                 | Source <sup>3</sup> | A <sup>4</sup> | R   | B | H | IC | C | X <sub>a</sub> | X <sub>b</sub> | X <sub>c</sub> | X <sub>d</sub> |
|--------------------------------------|---------------------|----------------|-----|---|---|----|---|----------------|----------------|----------------|----------------|
| <i>S. moritziana</i> Spring          | 1300                | + <sup>5</sup> | (+) | - | + | -  | - | -              | -              | -              | -              |
| <i>S. moritziana</i> Spring          | 1327                | +              | (+) | - | + | -  | - | -              | -              | -              | -              |
| <i>S. muscosa</i> Spring             | 1381                | +              | +   | - | + | +  | - | -              | -              | +              | -              |
| <i>S. popayanensis</i> Hieron.       | 1142                | +              | +   | - | + | +  | - | -              | -              | -              | -              |
| <i>S. popayanensis</i> Hieron.       | 1285                | +              | +   | - | + | +  | - | -              | -              | -              | -              |
| <i>S. porphyrospora</i> A. Braun     | 1268                | +              | +   | - | + | -  | - | -              | +              | -              | -              |
| <i>S. porphyrospora</i> A. Braun     | 1269                | +              | +   | - | + | -  | - | -              | +              | -              | -              |
| <i>S. porphyrospora</i> A. Braun     | 1281                | +              | +   | - | + | ?  | - | -              | +              | -              | -              |
| <i>S. seemannii</i> Baker            | 1357                | +              | +   | - | + | -  | - | -              | -              | +              | -              |
| <i>S. tenella</i> (P. Beauv.) Spring | 1367                | +              | +   | ? | + | ?  | - | -              | +              | -              | -              |

1. Separations were obtained on a Nucleosil C-18 column (4.6 mm × 250 mm i.d., 5  $\mu$ , Macherey & Nagel, Düren, Germany) at a flow rate of 1 ml/min using a linear gradient: 0 min: 60% solvent A in B, 30 min: 30% solvent A in B, 34 min: 30% solvent A in B; solvent A: 1% H<sub>3</sub>PO<sub>4</sub> in H<sub>2</sub>O; solvent B: MeCN. All separations were monitored at 220-440 nm.

2. Species arranged according to Jermy's (1986, 1990) classification.

3. Numbers without prefix correspond to Valdespino's collection numbers, BF = collected by Beat Fischer without number, L = extract provided by López-Sáez, N = Mike Nee's collection number, S = Carlos Sanchez' collection, NY (f = fresh, d = dried) = Early samples taken from the New York (NYBG) Propagation Range, PS = Mostly fresh phytochemical samples taken from the NYBG Propagation Range. Vouchers deposited at NY.

4. A = amentoflavone, B = bilobetin, C = cryptomerin B, H = hinokiflavone, IC = isocryptomerin, R = robustaflavone, X<sub>a</sub> = unknown a (RR<sub>t</sub> = 0.7-0.72 min), X<sub>b</sub> = unknown b (RR<sub>t</sub> = 0.83-0.85 min), X<sub>c</sub> = unknown c (RR<sub>t</sub> = 0.89-0.9 min), X<sub>d</sub> = unknown d (RR<sub>t</sub> = 1.18-1.19 min).

5. + = present, - = absent, (+) = trace ? = not clearly determined, co-chromatography dubious.

Table III  
CHROMATOGRAPHIC AND SPECTRAL CHARACTERISTICS OF BIFLAVONES IDENTIFIED FROM CRUDE EXTRACTS  
OF *SELAGINELLA* SPECIES

| Biflavones     | TLC <sup>1</sup> , color F <sub>254</sub> | UV <sub>366</sub> + AlCl <sub>3</sub> | HPLC <sup>2</sup> av. RR <sub>i</sub> <sup>3</sup><br>(min) | UV-absorption spectra <sup>4</sup><br>$\lambda_{\max}$ (nm) |
|----------------|-------------------------------------------|---------------------------------------|-------------------------------------------------------------|-------------------------------------------------------------|
| Amentoflavone  | Absorbing                                 | orange                                | 0.62                                                        | 267.5-335                                                   |
| Bilobetin      | Absorbing                                 | yellow                                | 0.85                                                        | 267-334                                                     |
| Robustaflavone | Absorbing                                 | yellow-orange                         | 0.68                                                        | 267.5-340                                                   |
| Hinokiflavone  | Absorbing                                 | yellow                                | 1.00                                                        | 267.5-337                                                   |
| Isocryptomerin | Absorbing                                 | yellow                                | 1.27                                                        | 269-335                                                     |
| Cryptomerin B  | Absorbing                                 | yellow                                | 1.67                                                        | 269-335                                                     |

1. TLC-system: toluene-EtOAc-HCOOH (5:4:1, 2x), silica gel F<sub>254</sub>

2. Separations: see Materials and Methods.

3. Average Relative Retention times: av. RR<sub>i</sub> =  $\frac{R_f(\text{other biflavones})}{R_f(\text{hinokiflavone})}$

4. UV-spectra were recorded in HPLC solvents A and B (see Materials and Methods) by photodiode array detection.



Figure 10. An example of a HPLC diagram obtained from a methanolic extract of Selaginella popayanensis (Valdespino 1142, NY), with expectrum index plot showing the UV-absorption spectra (220-440 nm) of each biflavone. The biflavones were identified by co-chromatography using the six authentic substances listed in Table III as internal standards. A = amentoflavone, H = hinokiflavone, IC = isocryptomerin, R = robustaflavone.

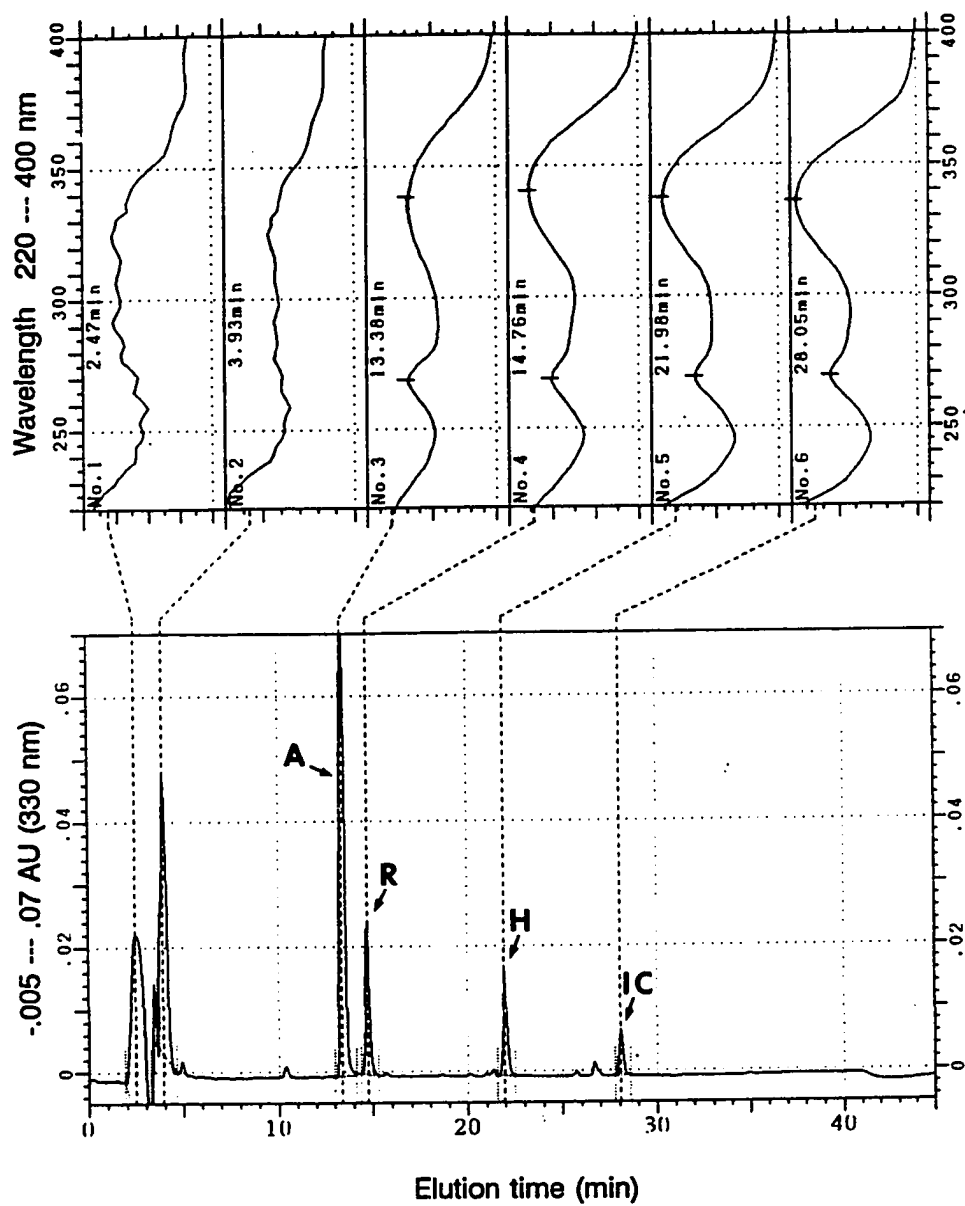
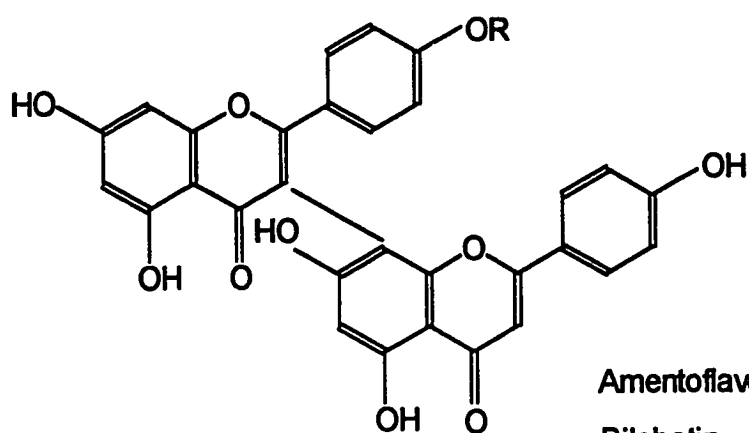
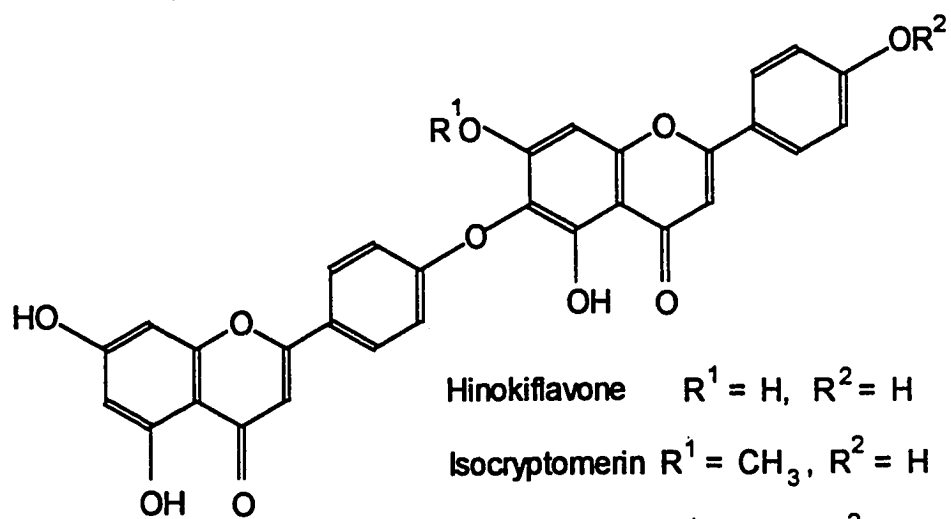
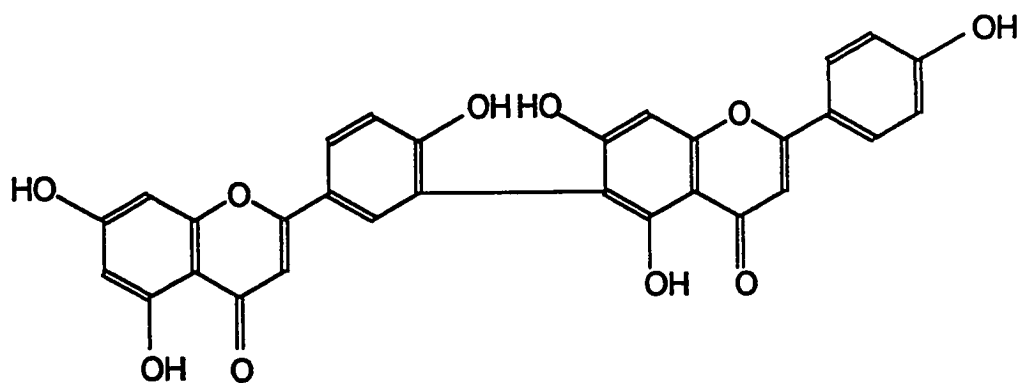


**Figure 11. Chemical structures of amentoflavone, hinokiflavone and their derivatives, as well as of robustaflavone.**

Amentoflavone  $R = H$ Bilobetin  $R = CH_3$ Hinokiflavone  $R^1 = H, R^2 = H$ Isocryptomerin  $R^1 = CH_3, R^2 = H$ Cryptomerin B  $R^1 = CH_3, R^2 = CH_3$ 

Robustaflavone

## CHAPTER VIII

## SUMMARY

Species of Selaginella subg. Heterostachys are chiefly characterized by lax, flattened, dorsiventral strobili, and dimorphic sporophylls. The dorsal sporophylls have an adaxial, laminal flap. This laminal flap is a projection on the dorsal sporophylls resulting from the partial fusion of the epidermal tissue of the adaxial surface. The laminal flap is not a structure developed de novo, but in fact the basiscopic margin of the dorsal sporophylls that is more or less perpendicular to the adaxial surface. The laminal flap is a character found in all New and Old World species of subg. Heterostachys thus far examined.

Leaf surface characters of vegetative leaves and sporophylls indicate that dorsal and ventral sporophylls are a continuation of the vegetative leaf rows, and therefore lend support to Goebel's (1905) hypothesis that dorsal and ventral sporophylls are modified median and lateral leaves, respectively.

Other morphological characters such as leaf idioblasts and the presence of hairs on the upper surface of the lateral leaves, are also characteristic of several neotropical taxa of subg. Heterostachys.

Species of subg. Heterostachys are widely distributed in Central and South America. Asexual reproduction mechanisms such as apogamy, formation of flagelliform stem and branch apices, buds, and stolons, are thought to enhance dispersal, and therefore distribution of some of the species studied. Species that

generally reproduce both sexually and asexually have a wider distribution than those that reproduce only sexually. According to this study most of the species studied have a wider distribution range than originally reported. It is believed that restricted distribution ranges in some species may be better explained as artifacts due to lack of critical collecting in many areas, rather than true endemism. Of the studied species only S. broadwayi is considered to be a true endemic in Trinidad, South America.

Megaspores of most of the examined species have the distal face variously reticulate and the proximal face smooth to slightly reticulate. Microspores of the studied species have the distal face baculate, clavate, echinate, or verrucate to gemmate. Variations on the exospore sculpturing and microstructure patterns of mega- and microspores are useful taxonomic characters to distinguish species and to determine species relationship. These patterns, however, are not exclusive of subg. Heterostachys, but are also found in species of subg. Heterostachys. Spore sculpturing and microstructure patterns, therefore, do not help define subg. Heterostachys.

Phytochemically, Selaginella is primarily characterized by the presence of the biflavones amentoflavone, hinokiflavone, and robustaflavone. Biflavones were present in all investigated species of Selaginella, including series Articulatae. The presence of biflavones seems to be a synapomorphy shared by Selaginella and most other groups of vascular plants (except for Lycopodiales, Isoëtales, Equisetales, and most of the ferns) and some moss families. The biflavonoid profile of species

of subg. Heterostachys does not provide any additional character to separate this subgenus from other heterophyllous and homophyllous species of Selaginella. The biflavone profile of both homophyllous and heterophyllous species investigated were similar. This evidence indicates that homophyllous and heterophyllous Selaginella are closely related and does not lend support to the taxonomic recognition of two separate genera.

In conclusion, dimorphic sporophylls, the presence of laminal flap, leaf idioblasts, and hairs on the upper surface of the lateral leaves may be synapomorphies that support subg. Heterostachys as a monophyletic group regardless of overall classification of Selaginella.

## CHAPTER VIII

TAXONOMIC REVISION OF *SELAGINELLA*SUBGENUS *HETEROSTACHYS* IN CENTRAL AND SOUTH AMERICA

"Une des causes principales de la confusion qui règne dans la détermination des espèces des Lycopodiacees, vient de ce que les descriptions de la plupart des auteurs qui en ont traité, ne consistent qu'en phrases courtes et peu caractéristiques."

A. F. Spring, *Mém. Acad. Roy. Sci. Belgique* (15: 5. 1842)

## VII. 1. INTRODUCTION

More than a century and a half has elapsed since Spring made the remarks quoted above, yet they are as valid now as they were then. Since Spring's (1849) major monograph of the genus *Selaginella*, no other botanist has provided such a complete and thorough account of the genus. After Spring, however, some students of the genus reverted to the deplorable practice of providing only brief descriptions, very often mentioning uninformative characteristics as previously complained about by Spring. Thus, I thought it necessary to provide thorough descriptions for the species treated in this monograph. For some botanists these descriptions may be too long. I will argue against this assertion only by citing, as did Spring before me, the following: "Nullum vocabulum in differentia specifica superfluum erit" (Linneaus, *Philos. Bot.* 1751: 292).

When appropriate, I have also made an effort to provide discussions in nomenclatural and taxonomic matters. These discussions as well as the species descriptions are based on examination of type collections cited here and on a large



number of specimens from different European, North American, and Latin American herbaria, which have been cited in the Acknowledgments section.

In many cases species names were in need of lectotypification and since I have seen all the type material involved, unless otherwise stated, they are lectotypified here. In few cases, where I did not see all type material, I defer lectotypification until additional studies can be carried out and all type material seen.

The subgeneric description is provided as to include those characteristics common to Central and South American species of subg. Heterostachys. The species descriptions that come after the subgeneric description were made by studying herbarium specimens, using leaf clearings, SEM preparation of leaves from selected species, and LM and SEM spore studies in selected taxa. ♦

In general, measurements of lateral and median leaves were obtained from leaves on the main stem, and those of the strobili and sporophylls from mature strobili. Measurements of leaf width were taken at the widest point including both margin and excluding any projection of the margins (i.e., cilia or teeth). Measurements of leaf length were taken from the base to the tip, except on the median leaves where the arista or acumen were measured separately.

Measurements were made using a stereomicroscope Bausch & Lomb Stereozoom 7, Zoom Range 10-70 $\times$ ., and a Nikon light microscope Model L-Ke, both equipped with ocular micrometers.

**Selaginella** P. Beauvois, Mag. Encycl. 5: 478. 1804; Prodr. Aethéogam., 101.

1805, nomen conserv.

Type: Selaginella selaginoides (L.) P. Beauvois ex Schrank & Martius, Hort.

Reg. Monac. 1: 182. 1829.

**Selaginella** P. Beauvois subg. **Heterostachys** Baker, J. Bot. 21: 4. 1883.

Lectotype (chosen by Jermy, 1986): Selaginella heterostachys Baker, J. Bot.

23: 177. 1885.

Selaginella P. Beauvois subg. Heterophyllum Hieronymus series Monostelicae

Hieronymus in Engler & Prantl, Nat. Pflanzenfam. 1 (4): 673. 1901, p.p.

Plants terrestrial, epipetric, or epiphytic. Stems creeping, ascending to suberect, stramineous to chlorophyllous, not articulate, 1-4-branched. Rhizophores axillary or ventro-axillary. Leaves dimorphic throughout, thin-membranous or membranous, the upper surface green, composed of rounded cells with sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls, both surfaces with or without idioblasts. Strobili terminal on branch tips, lax, flattened, and dorsiventral. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, occasionally puberulent or glabrous, with or without idioblasts, the lower surface silvery to

silvery green, composed of elongate cells with sinuate walls; ventral sporophylls pale green to hyaline, ascending to spreading, pseudopeltately attached to the axis, frequently without an adaxial flap, both surfaces composed of elongate, hyaline cells with sinuate walls, frequently glabrous, with or without idioblasts.

31 species in Central and South America.

Key to the species of Selaginella P. Beauv. subg. Heterostachys Baker  
in Central and South America

1. Acroscopic margin of the lateral leaves ciliate to ciliate-denticulate at least along basal  $\frac{1}{4}$ .
2. Upper surface of the lateral leaves with idioblasts.
3. Median leaves with an outer auricle well defined and free from the stem; lateral leaves with the basiscopic margin usually long-ciliate at proximal base; stems stoloniferous.
4. Acroscopic margin of the lateral leaves long-ciliate, ciliate-denticulate, or serrate along basal  $\frac{1}{3}$ , the cilia or teeth length less than  $\frac{1}{4}$  the width of the lamina; stem and branch apices frequently flagelliform.....  
.....23. S. lineolata
4. Acroscopic margin of the lateral leaves long-ciliate along basal  $\frac{2}{3}$  to  $\frac{1}{2}$ ,

the cilia length more than  $\frac{1}{4}$  the width of the lamina; stem and branch apices usually not flagelliform.....22. S. prolifera

3. Median leaves without an outer auricle; lateral leaves with the basiscope margin usually serrate to entire; stems without stolons or occasionally stoloniferous.

5. Arista of the median leaves less than  $\frac{1}{4}$  the length of the lamina, or if  $\frac{1}{4}$  the length of the lamina then upper surface of leaves rugose to rugulate and lateral leaves hispid near the basiscope margin.

6. Median leaves lanceolate; lateral leaves with the apex obtuse, the upper surface with inconspicuous hairs near the basiscope margin or glabrous; upper surface of leaves smooth; megaspores pinard to baryta yellow.....5. S. hyalogramma

6. Median leaves broadly ovate, ovate-deltate, or ovate-orbicular; lateral leaves with the apex acute or short- to long-acuminate, the upper surface frequently hispid near the basiscope margin; upper surface of leaves rugose to rugulate; megaspores orange-buff, light orange-yellow, or deep chrome.....15. S. moritziana

5. Arista of the median leaves  $\frac{1}{4}$  or  $\frac{1}{2}$  the length of the lamina.

7. Lateral leaves usually with one or two, large idioblasts resembling veins on the upper or lower surface, the upper surface with short hairs near the basiscope margin; megaspores orange.....19. S. porphyrospora

7. Lateral leaves usually with many, short idioblasts on the upper surface

and occasionally on the lower surface, the upper surface glabrous; megaspores white (in S. tenella), baryta- to empire yellow or white (in S. muscosa).

8. Apex of stem and branches frequently flagelliform; median leaves elliptic to narrowly elliptic, the base oblique, the margins sparsely serrate.....29. S. tenella

8. Apex of stem and branches not flagelliform; median leaves broadly ovate to ovate-lanceolate, the base asymmetric with the inner base truncate and the outer base weakly auricled, subcordate, or rounded, the margins short-ciliate along proximal  $\frac{3}{4}$ , serrate to serrulate apically.....6. S. muscosa

2. Upper surface of the lateral leaves without idioblasts.

9. Lateral leaves semicordiform to cordiform; median leaves cordiform to ovate-deltate.....7. S. porelloides

9. Lateral leaves ovate, ovate-orbicular, ovate-lanceolate, lanceolate, ovate-oblong, oblong, or ovate-elliptic; median leaves ovate, ovate-lanceolate, lanceolate, elliptic, elliptic-orbicular, or if ovate-deltate then the apex broadly acute and ciliate at tip.

10. Median leaves with a prominent and ciliate outer auricle.

11. Lateral leaves with the midrib raised and frequently hyaline; median leaves with a well developed and long-ciliate inner auricle.....25. S. tuberosa

11. Lateral leaves with the midrib not prominent, or distinctly hyaline;  
median leaves with neither a well developed nor ciliate inner  
auricle.....24. S. finitima
10. Median leaves without a prominent outer auricle.
12. Median leaves ovate-orbicular to ovate-deltate; leaves from basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of  
the stem with the margins fimbriate, the apices obtuse or broadly acute,  
ciliate at tip.....30. S. leucoloma
12. Median leaves ovate, ovate-lanceolate, lanceolate, elliptic, or ovate-elliptic;  
leaves from basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem with the margins serrulate to ciliate,  
the apices acute to acuminate, or aristate, dentate at tip.
13. Median leaves elliptic or ovate-elliptic.
14. Lateral leaves with an acuminate apex; upper surface of the median  
leaves without idioblasts; megaspores massicot to naphthalene  
yellow (lemon yellow).....31. S. sobolifera
14. Lateral leaves with a broadly acute to obtuse apex; upper surface  
of the median leaves with conspicuous to obscure idioblasts;  
megaspores light to maize yellow, cream, pale yellow-orange, or  
pale orange-yellow.
15. Median leaves aristate, the arista  $\frac{1}{2}$  or more the length of the  
lamina, 0.6-1.5 mm long; upper surface of the lateral leaves  
frequently with few, long hairs; megaspores maize yellow,  
cream, pale yellow-orange, or pale orange-yellow.....

- .....11. S. lychnuchus
15. Median leaves acute to shortly acuminate, the acumen when present less than  $\frac{1}{4}$  the length of the lamina, 0.1-0.26 mm long; upper of the lateral leaves glabrous; megaspores marguerite yellow (light yellow).....9. S. gynostachya
13. Median leaves ovate, ovate-lanceolate, or lanceolate.
16. Median leaves of basal  $\frac{1}{2}$  of the stem with the margins long-ciliate; upright stems developing from basal tuber-like buds covered with long-ciliate to fimbriate, whitish or reddish, scale-like leaves.....21. S. mixteca
16. Median leaves throughout the stem with the margins serrulate, serrate, or ciliate-denticulate; upright stems not developing from tuber-like buds, if stoloniferous then covered with serrate, greenish scale-like leaves.
17. Stems creeping to ascending, stoloniferous, occasionally flagelliform; lateral leaves with the acroscopic margin serrate or infrequently ciliate-denticulate along basal  $\frac{1}{4}$ .....16. S. flacca
17. Stems ascending to suberect, not stoloniferous nor flagelliform; lateral leaves with the acroscopic margin short- to long-ciliate along basal  $\frac{1}{4}$  to  $\frac{2}{3}$ .
18. Median leaves lanceolate to lance-ovate, the base rounded; megaspores pinard yellow.....3. S. simplex
18. Median leaves ovate to ovate-lanceolate, the base asymmetric, the inner base truncate and the outer base decurrent to form

a very weakly differentiated auricle or ventricose outer base;  
megaspores snow-white or with white ridges over a marguerite  
to primrose yellow background.

19. Median leaves ovate, the margins conspicuously hyaline; upper surface  
of the median leaves and dorsal sporophylls usually with conspicuous  
stomata throughout; dorsal sporophylls with the margins serrate to  
serrulate or ciliate-denticulate; megaspores snow-white.....1. S. minima

19. Median leaves ovate to ovate-lanceolate, the margins obscurely hyaline;  
upper surface of the median leaves and dorsal sporophylls usually with  
obscure stomata; dorsal sporophylls usually with the margin long-  
ciliate; megaspores with white ridges over a marguerite to primrose  
yellow background.....2. S. broadwayi

1. Acroscopic margin of the lateral leaves serrate to serrulate or entire near  
the base or throughout.

20. Upper surface of lateral and median leaves with idioblasts, or idioblasts  
restricted to the upper surface of the lateral leaves only, or idioblasts  
present on the upper surface of the median leaves and/or on the lower  
surface of the lateral leaves.

21. Median leaves with at least the outer base well developed into an  
auricle free from the stem; rhizophores stout, 0.3-0.86 mm diam.

22. Lateral leaves, when old, brownish and frequently clasping the  
stem; median leaves frequently with two distinct and free from



the stem auricles, or the outer auricle more developed than the inner one, the auricles ciliate-denticulate or long-ciliate, the apex long-aristate, the arista more than  $\frac{1}{4}$  the length of the lamina.....28. S. stenophylla

22. Lateral leaves, when old, greenish and perpendicular to the stem; median leaves with only the outer base auricled, free from the stem, the inner base rounded, weakly distinct from the stem, both the inner and the outer base entire to serrulate, the apex acuminate to short-aristate, the arista  $\frac{1}{4}$  or less the length of the lamina.....10. S. karowtipuensis

21. Median leaves with the outer base asymmetric, rounded, oblique, or subcordate, if with an outer auricle then this not distinctly free from the stem; rhizophores thin to stout, 0.08-0.56 mm diam.

23. Lateral leaves usually with one or two, large idioblasts resembling veins on the upper or lower surface; microspores usually reddish.....19. S. porphyrospora

23. Lateral leaves usually with many, short idioblasts on the upper surface and occasionally on the lower surface or only on the lower surface; microspores light to deep orange.

24. Median leaves broadly ovate, ovate-deltate, or ovate-orbicular, the upper surface usually rugose to rugulate or irregularly smooth; upper surface of the lateral leaves frequently with short hairs near

- the basiscopic margin; leaves usually deep green to deep blue-green.....15. S. moritziana
24. Median leaves lanceolate, ovate-lanceolate, broadly ovate, elliptic, or ovate-elliptic, the upper surface usually smooth; upper surface of the lateral leaves glabrous; leaves light-green to light blue-green.
25. Apex of the lateral leaves obtuse to broadly acute; apex of the median leaves acute to shortly acuminate, the acumen  $\frac{1}{8}$  or less the length of the lamina.
26. Stems ascending to suberect; median leaves lanceolate; lateral leaves broadly ovate to ovate-lanceolate, with the base rounded to semicordate.....5. S. hyalogramma
26. Stems creeping; median leaves elliptic to ovate-elliptic or broadly ovate; lateral leaves oblong to oblong-ovate or broadly ovate, with the base truncate to rounded.....9. S. gynostachya
25. Apex of the lateral leaves acute to shortly acuminate; apex of the median leaves long-acuminate to long-aristate, the acumen or arista  $\frac{1}{4}$  or usually more the length of the lamina.
27. Apex of the stem and branches frequently flagelliform; median leaves elliptic to narrowly elliptic, the base oblique, the margins sparsely serrate.....29. S. tenella
27. Apex of the stem and branches not flagelliform; median

leaves broadly-ovate to ovate-lanceolate, the base asymmetric with the inner base truncate and the outer base weakly auricled, subcordate, or rounded, the margins short-ciliate along proximal  $\frac{3}{4}$ , serrate to serrulate apically.....6. S. muscosa

20. Upper surface of the lateral and median leaves without idioblasts or idioblasts only on the upper surface of the median leaves.

28. Median leaves obovate.....20. S. glossophylla

28. Median leaves elliptic, ovate-elliptic, ovate, or ovate-lanceolate.

29. Median leaves with the outer base well developed into an auricle  
.....8. S. seemannii

29. Median leaves with the outer base asymmetric, oblique, or semicordate, without a well developed auricle.

30. Lateral leaves with the upper surface usually hispid throughout or with short hairs near the basiscopic margin; upper surface of dorsal sporophylls glabrous or with short hairs.

31. Lateral leaves thin-membranous, the upper surface hispid throughout; upper surface of dorsal sporophylls glabrous; megaspores whitish.....4. S. correae

31. Lateral leaves thin, the upper surface usually with short hairs near the basiscopic margin; upper surface of dorsal sporophylls usually with short hairs;

megaspores orange-buff, light orange yellow, deep chrome, or cream.

32. Median leaves ovate-lanceolate, with stomata along midrib, the apex acute or gradually short- to long-acuminate, the acumen  $\frac{1}{4}$  or less the length of the lamina; megaspores orange-buff, light orange yellow, deep chrome.....

.....14. S. popayanensis

32. Median leaves ovate-elliptic, with stomata along midrib and throughout the lamina, the apex abruptly aristate, the arista  $\frac{1}{4}$  or more the length of the lamina; megaspores cream.....18. S. bernoullii

30. Lateral leaves with the upper surface glabrous, or if hairs present these inconspicuous; dorsal sporophylls glabrous.

33. Median leaves with the apex acute, acuminate, or short-aristate, the acumen or arista  $\frac{1}{3}$  or less the length of the lamina.

34. Upper surface of median leaves and dorsal sporophylls with stomata throughout; lateral leaves oblong to oblong-ovate, 2.8-4 mm long.....

.....9. S. gynostachya

34. Upper surface of median leaves and dorsal sporophylls with stomata along midrib and frequently along the basal  $\frac{1}{2}$  near the outer margin; lateral leaves ovate, ovate-elliptic, or ovate-oblong, 1.3-2.7 mm long.

35. Median leaves broadly elliptic or obovate-elliptic, the apex abruptly aristate; megaspores snow-white.....26. S. macilenta

35. Median leaves ovate, ovate-lanceolate, or lanceolate, the apex gradually short-acuminate to short-aristate; megaspores orange-buff, light orange-yellow, or yellow.
36. Lateral leaves broadly ovate or broadly ovate-elliptic, the apex obtuse to broadly acute, or occasionally abruptly acute; sporophylls usually broadly ovate.....17. S. cavifolia
36. Lateral leaves ovate-elliptic or ovate-oblong, the apex short- to long-acuminate; sporophylls lanceolate to lance-ovate..  
.....16. S. flacca
33. Median leaves with the apex long-aristate, the arista more than  $\frac{1}{3}$  the length of the lamina.
37. Lateral leaves broadly ovate; median leaves broadly ovate; megaspores snow-white.....27. S. flagellata
37. Lateral leaves ovate, ovate-oblong, or oblong; median leaves narrowly elliptic or narrowly elliptic-ovate; megaspores cream, marguerite yellow, massicot to naphthalene yellow, or orange-buff.
38. Base of the stem lacking stolons, without tuber-like buds; apex of the stem and branches usually not flagelliform; megaspores cream to marguerite yellow; dorsal sporophylls asymmetric, oblong to oblong-lanceolate, or oblong-ovate.....12. S. ramosissima
38. Base of the stem stoloniferous, forming tuber-like buds at tip; apex of the stem and branches occasionally or frequently flagelliform;

megaspores massicot to naphthalene yellow, or orange-buff;  
dorsal sporophylls asymmetric, lanceolate, lance-ovate, or ovate.

39. Median leaves with the arista 0.5-0.7 mm long; apex of the  
stem occasionally flagelliform; megaspores orange-buff;  
distal face of the microspores seemingly smooth or papillate  
.....13. S. chionoloma

39. Median leaves with the arista 0.16-0.46 mm long; apex of the  
stem frequently flagelliform; megaspores massicot to  
naphthalene yellow; distal face of the microspores baculate  
to clavate.....31. S. sobolifera

1. *Selaginella minima* Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 139. 1843.

Type: FRENCH GUIANA. Leprieur s.n. (Lectotype: LG!, here designated; isolectotype: P!). (Figs. 5A-D; 9I & J; 12A-E).

Selaginella cruegeri Jenman, Gard. Chron. III, 22: 378. 1897 (as "crugerii"), **syn. nov.**

Type: TRINIDAD. ST. GEORGE Co.: Arouca?, 15 Dec 1851, Herb. Trin. No. 194 (Holotype: TRIN!; isotype: B!, US!).

Selaginella tropidophora Mickel & Beitel, Mem. New York Bot. Gard. 46: 354. 1988, **syn. nov.**

Type. MEXICO. OAXACA: Distrito Tuxtepec, 1-3 km S of Usila, 1000' [300 m], 27 Sep 1973, Mickel 7392 (Holotype: NY!; isotypes; none seen [in the original publication isotypes were reported "to be distributed." The collection data of the holotype as cited by Mickel and Beitel (1988) are incorrect, being that of the paratype Mickel 4204]).

Plants terrestrial. Stems ascending to suberect, stramineous to chlorophyllous, 1-9 cm long, 0.2-0.5(-0.8) mm diam., not articulate, not flagelliform, not stoloniferous, 1-3-branched. Rhizophores axillary, restricted to the basal ½ of the stem, filiform, 0.08-0.22 mm diam. Leaves dimorphic throughout, thin-membranous, the upper surface green, composed of rounded cells with sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant, perpendicular to the stem, ovate to broadly

ovate, 1.5-1.9 × 0.8-1.1 mm; base rounded, the acroscopic base strongly overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin obscurely or conspicuously hyaline, or greenish, long-ciliate along basal  $\frac{2}{3}$ , serrate to serrulate apically, the basiscopic margin hyaline or greenish, entire to serrulate (especially along apical  $\frac{1}{2}$ ); apex acute, dentate at tip; the upper surface frequently with sparse short hairs or glabrescent, without idioblasts or conspicuous stomata, the lower surface glabrous, without conspicuous idioblasts or stomata. Median leaves distant, ascending, ovate, 1-1.3 × 0.45-0.7(-0.8) mm; base asymmetric with the inner base truncate and the outer base decurrent to form a weakly differentiated outer auricle, or oblique; margins conspicuously hyaline, serrate to serrulate, or the outer margin short ciliate along basal  $\frac{1}{2}$  and serrate to serrulate along apical  $\frac{1}{2}$  and the inner margin serrate to serrulate; apex acute to long-acuminate, dentate at tip; both surfaces glabrous, without conspicuous idioblasts, the upper surface frequently with conspicuous stomata throughout, or these obscure, the lower surface without conspicuous stomata. Axillary leaves similar to lateral leaves, except for the margins which are long-ciliate along the basal  $\frac{1}{2}$  or  $\frac{1}{4}$  and serrate to serrulate apically. Strobili terminal on branch tips, lax, flattened, and dorsiventral, 2-5(-12) mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along ca.  $\frac{1}{2}$  to  $\frac{2}{3}$  the sporophyll length, asymmetric to ovate-lanceolate, 1.3-1.98 × 0.4-0.7 mm, with a strongly developed denticulate keel along midrib, the base rounded, the margins hyaline, sparsely serrate to serrulate, or inner margin



sparsely serrate to serrulate and outer margin ciliate-denticulate along basal  $\frac{1}{3}$ , sparsely serrate, serrulate to entire apically, the apex acute to shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, occasionally puberulent or glabrous, without idioblasts, with conspicuous stomata throughout or this obscure, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls; ventral sporophylls almost pale green to hyaline, ascending to spreading, pseudopeltately attached to the axis, frequently with a slightly developed adaxial flap, ovate to broadly ovate, (1-)1.4-1.92  $\times$  0.5-0.76 mm, with a well developed denticulate to entire keel along midrib, the base rounded, the margins hyaline, long to short-ciliate, the apex acute to long-acuminate, both surfaces composed of elongate, hyaline cells with sinuate walls, glabrous, without conspicuous idioblasts or stomata. Megasporangia in two ventral rows or sometimes mixed in one of these rows with microsporangia; megaspores snow-white, frequently with a slightly developed equatorial flange or this absent, the proximal face rugulate, striate-reticulate to reticulate with open to close reticulum of low ridges, the distal face rugulate to rugulate-reticulate or reticulate with open reticulum of low ridges [see A. Tryon & Lugardon, 1991: 614-615, for comparison with striate ornamentation on proximal face], 270-350  $\mu$ m diam. Microsporangia usually in two dorsal rows, sometimes mixed with megasporangia in a ventral row, absent from dorsal rows, or only one dorsal and basal, if absent then dorsal sporophylls sterile; microspores tan, without an equatorial flange, the proximal and

distal faces with verrucate to gemmate projections covered with micro-echini, 45-50  $\mu\text{m}$  diam.

**HABITAT AND DISTRIBUTION:** On dry and open wooded slopes, savanna on clay banks, rocky cerrado on shaded stream banks; 100-1000 m; Mexico, Honduras, Nicaragua, Panama, Venezuela, Trinidad, French Guiana, Brazil, and Bolivia.

**SPECIMENS EXAMINED:** MEXICO: OAXACA: Juchitán, Isthmus of Tehuantepec, 6 km N of Matías Romero, 1000' [300 m], 19 Oct 1969, Mickel & Hellwig 4204 (NY, UC); 3 km of Matías Romero, 17 Dec 1972, R. Tryon & A. Tryon 7389 (7389a at GH); Tuxtepec, 1-3 km S of Usila, 1000' [300 m], 27 Sep 1973, Mickel 7392 (NY!, type coll. of S. tropidophora).

HONDURAS. GRACIAS A DIOS: La Mosquitia, Ahuas, 15°30'N, 84°20'W, 12-14 Dec 1972, Clewell 3657 (TEFH).

NICARAGUA. In the plains of northeastern Nicaragua, s.d., Gómez s.n. and comm. to McAlpin (21 Apr 1978, McAlpin s.n., at NY).

PANAMA. PANAMA': Perlas Archipelago, Gulf of Panamá, ca. 55 miles [88.5 km] SSE of Balboa, San José Island, Bald Hill, 29 Oct 1944, Johnston 327 (GH), San José Island, 24 Dec 1945, Johnston 878 (GH, MO, PMA, S, U, US).

VENEZUELA. GUÁRICO: Infante, Parque Nacional Aguaro-Guariquito, Morichal Indio Viejo, 9°48'-9°52'N, 67°52'-67°56'W, 100 m, Dec 1981, Delascio et al. 11512 (MO).

TRINIDAD. St. Ann, 28 Oct 1923, Broadway s.n. (BM, NY). Arouca [Aronca?], 15 Dec 1851, Herb. Trin. No. 194 (TRIN, US, type coll. of S. cruegeri). Aripo savanna, 120' [36 m], 23 Dec 1959, Richardson 792 (TRIN). O'Meara savanna, 22 Mar 1921, Britton & Britton 2495 (NY, TRIN). Piarco Savanna, 13 Dec 1907, Broadway 2150 (Z).

FRENCH GUIANA: Leprieur s.n. (LG, P, lectotype of S. minima); In planitiebus humides Insulae Cayenne, Août [Aug] 1831 or 1833?, Leprieur 13 (G, L); In planitiebus herbosis, hieme inundatis, ad basin montis Tigre, Insulae Cayenne, Août [Aug] 1837. Leprieur s.n. [1839.7, 158] (P, US); 1839, Leprieur 7 (G); In herbosis, hieme, circa Cayenne, Leprieur s.n. (K).

BRAZIL. CEARÁ: Cedro, 17 Jun 1912, Loefgren 1160 (BM, R). GOIÁS: 4 km by road E of São João da Alança, 1000 m, 24 Mar 1973, Anderson 7863 (K, NY). MATO GROSSO: ca. 20 km ENE of Barra do Garças, 460 m, 6 May 1973, Anderson 9859 (K, NY). RONDÔNIA: 37 km S of Huamaitá along highway to Pôrto Velho, 6 May 1982, McFarland et al. 79 (NY). RORAIMA: Alto Alegre, Reserva Ecológica de Maracá, Santa Rosa Campo, NE of SEMA Research Station buildings, ca. 80 m, 7 Mar 1987, Edwards 2489 (BM). WITHOUT SPECIFIC STATE OR LOCALITY: Burchell 7006 (K p.p.).

BOLIVIA. SANTA CRUZ: Velasco, campamento Las Torres, margen del Río Iténez (Guaporé), frontera con Mato Grosso, NE Serrania Huanchaca, 24 km S de Flor de Oro, ca. 50 km N del Río Verde, 13°39'S, 60°48'W, 200-400 m, 24 May 1991, Peña & R. Foster 210 (F).

NOMENCLATURAL COMMENTS: There are some problems regarding the type collection of S. minima, which I believe warrant its lectotypification. In the protologue, Spring (1843) cited as the locality and collector: "Hab. in Guyana gallica (Leprieur).". Later Spring (1849) cited: "Hab. in Guyana gallica [in planitiibus humidis prope Cayenne, fr. Aug.: Leprieur (H.M.P., H. Deless., H. Hooker)]". Alston et al. (1981) cited as the type: "French Guiana: ad basin montis Eigre [Tigre?] Insulae Cayenne, Leprieur 158," and almost all other authors have followed this citation (e.g., Lellinger, 1989), or with some modifications (e.g., Fraile (in Fraile et al.), in press; Mickel & Beitel, 1988). It is difficult to ascertain which of these specimens cited by previous authors should be considered the holotype, because all of them were collected by Leprieur in French Guiana, some were annotated by Spring, all represent the same species, and the original citation is vague. According to Article 9.9 of the ICBN (Greuter, 1994), since no holotype was indicated by the author a lectotype may be designated from among the original material. Among the collections cited by Spring (1843 and 1849), only two specimens, apparently representing the same collection and annotated by Spring, match the original protologue the best; one is found at P! and the other at LG!. Badré (1983) considered the specimen at LG to be the holotype, which could be considered an unintentional lectotypification. I have examined the aforementioned specimens and conclude that they agree with the original protologue and in the absence of any obstacle I confirm Badré's lectotypification here.

I have examined the specimen at NY cited by Mickel and Beitel (1988) as an isotype of S. minima, and conclude that it is not this species but probably S. armata Baker from the West Indies. It has been excluded, therefore, as type material.

I have also examined the types of S. tropidophora Mickel & Beitel and S. cruegeri Jenman, and found both to be conspecific with S. minima, and therefore I have reduced them to synonymy. There may be some confusion regarding the type collection of S. cruegeri. Jenman (1897) cited as the type of S. cruegeri "No. 194, Herb. Trin.," and I have seen two herbarium sheets at TRIN with this number. Upon careful study, I consider as holotype the specimen that bears in Jenman's handwriting the abbreviation "sp. nov." in addition to a brief diagnosis, probably also by Jenman, and which agrees with the original protologue. The other herbarium sheet is probably S. confusa Baker, and was apparently a later addition according to a handwritten note by Jenman glued onto it.

TAXONOMIC DISCUSSION: Because of its small size S. minima has been very often confused with S. simplex (Valdespino, 1993b). However, it is easily distinguished from it by the characters given in the key (see discussion of S. simplex). Selaginella minima is very closely related to and may be difficult to separate from S. broadwayi. Specimens of S. minima, (e.g., Peña & R. Foster 210, Johnston 878), frequently have short hairs on the upper surface of lateral leaves and sporophylls, and conspicuous stomata on the upper surface of median leaves

and dorsal sporophylls, whereas in S. broadwayi the lateral leaves and upper sporophylls are glabrous, and the upper surface of median leaves and dorsal sporophylls have obscure stomata. Further discussion about these two species is found under S. broadwayi.

A specimen from Brazil, Loefgren 1160 (BM, R) is unusual in that it has the margins of the leaves and sporophylls only serrate to serrulate, and the base of median leaf is rounded or with the outer base weakly developed into an obscure auricle. Nevertheless, it matches the other specimens in all other characters, and therefore it is included here.

In S. minima the strobili sometimes contain only megasporangia. This trait is also found in several other species of subg. Heterostachys treated in this monograph, and seems to be a more common phenomenon among members of subg. Heterostachys than previously realized (see discussion under S. porphyrospora). The same condition has been reported by Kornaś and Jankun (1983) for S. tenerrima A. Braun ex Kuhnby, an African member of subg. Heterostachys. In this species strobili usually have only megasporangia, and megaspores germinate without fertilization, effectively reproducing by apogamy. Kornaś and Jankun speculated that this mechanism was developed as a possible adaptation to periods of drought. This, however, contradicts Geiger's (1934) hypothesis that in S. anocardia (= S. muscosa) apogamy was dependent on a very moist and shady environment; see also Ruf's thesis (1976) for additional comments in this topic, where there is reference to experiments carried out by Goebel on S.

anocardia, demonstrating that it reproduces by apogamy. This evidence suggests that some of the species in subg. Heterostachys may have facultative asexual reproduction by apogamy influenced by environmental conditions. Hieronymus (1911) has speculated that apogamy has played an important role in the wide distribution of some species. Indeed, this type of reproduction may account for the wide distribution found in some species of subg. Heterostachys, e.g., S. porphyrospora, S. flagellata, S. muscosa, among others. Theoretically, it would be easier for one spore (a megaspore) to be dispersed by rain or other agents (e.g., animals), and germinate into an apomictic gametophyte. This gametophyte can, in turn, establish a new population, rather than requiring both mega- and microspores simultaneously dispersed to found a new population after fertilization. Successful gene flow, of course, between the original sexual population or other sexual population and the newly formed apomictic population will have to take place in order for the latter to be able to form sexual colonies or populations with a different distribution.

Fig. 12. A-E. Selaginella minima (Mickel 4204, NY). A. Habit. B. Upper surface of branch, with dorsal side of the strobilus. C. Lower surface of branch, with ventral side of the strobilus. D. Median leaves. E. Axillary leaf. F. Lateral leaf.





**2. *Selaginella broadwayi* Hieronymus, Hedwigia 58: 317. 1917. (Figs. 9G & H).**

Type: TRINIDAD. ST. GEORGE CO.: Government house, 18 Nov 1907,

Broadway 1934 (Holotype: B-n.v.; isotypes: BM!, BR!, G!, MO!, NY!, US!).

Plants terrestrial. Stems ascending to suberect, stramineous, (1-)1.3-2.5 cm long, 0.14-0.2 mm diam., not articulate, not flagelliform, not stoloniferous, not or 1-branched. Rhizophores axillary, restricted to the basal  $\frac{1}{4}$  or  $\frac{1}{2}$  of the stem, filiform, 0.06-0.1 mm diam. Leaves dimorphic throughout, thin-membranous, the upper surface green, composed of rounded cells with sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant, perpendicular to the stem, ovate or ovate-lanceolate,  $1.4-1.9 \times 0.6-1.3$  mm; base rounded, the acroscopic base slightly to strongly overlapping the stem, the basisopic base not overlapping the stem; the acroscopic margin pale green or obscurely hyaline, long-ciliate along basal  $\frac{1}{4}$  to  $\frac{1}{3}$ , serrate to serrulate apically, the basisopic margin hyaline, entire to serrulate, or occasionally shortly ciliate along basal  $\frac{1}{4}$  and entire to serrulate apically; apex acute, dentate at tip; the upper surface glabrous, without idioblasts or conspicuous stomata, the lower surface glabrous, without conspicuous idioblasts, with stomata throughout. Median leaves distant, ascending, ovate to ovate-lanceolate,  $0.8-1.2 \times 0.48-0.68$  mm; base asymmetric with the inner base slightly truncate and the outer base decurrent to form a weakly differentiated outer auricle, oblique, or rounded; margins obscurely hyaline, serrulate; apex long-acuminate to aristate, the acumen or arista  $\frac{1}{4}$  or less

the length of the lamina, 0.1-0.2 mm long, dentate at tip, both surfaces glabrous, without conspicuous idioblasts, the upper surface with obscure stomata along midrib, the lower surface without evident stomata. Axillary leaves similar to lateral leaves, except for the margins long-ciliate along basal  $\frac{1}{2}$  or  $\frac{1}{4}$  and serrate to serrulate apically. Strobili terminal on branch tips, lax and flattened, dorsiventral, 2-6 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial laminal flap extending along  $\frac{3}{4}$  or throughout the sporophyll length, asymmetric or lanceolate to lance-ovate,  $1.5-2.1 \times 0.5-0.92$  mm, with a strongly developed denticulate keel along midrib, especially along apical  $\frac{1}{2}$ , the base rounded, the margins hyaline, long-ciliate, ciliate-denticulate, serrate (by breaking off of cilia) along basal part, or inner margin serrate and outer margin long-ciliate, the apex acute to short-acuminate, the upper surface green, composed of rounded cells with sinuate walls, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts, with or without conspicuous stomata, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, with idioblasts, and without stomata; ventral sporophylls mostly completely hyaline, ascending, pseudopeltately attached to the axis, without an adaxial flap, lanceolate to ovate-lanceolate, or ovate,  $1.3-1.6 \times 0.5-0.76$  mm, with a slightly developed and entire keel along midrib, the base rounded, the margins hyaline, long-ciliate, the apex long-acuminate to aristate, both surfaces made of elongate, hyaline cells with sinuate walls, glabrous, with obscure to conspicuous

idioblasts, the stomata present only on the lower surface. Megasporangia in two ventral rows; megaspores with white ridges over a marguerite yellow to primrose yellow background, with or without a slightly developed equatorial flange, the proximal face granulate or granulate-reticulate with open reticulum of low ridges, the distal face reticulate with open reticulum of moderately high ridges, 215-240  $\mu\text{m}$  diam. Microsporangia in two dorsal rows; microspores tan, without an equatorial flange, the proximal and distal faces with smooth, gemmate to clavate projections, 25-30  $\mu\text{m}$  diam.

HABITAT AND DISTRIBUTION: Among grass on open or shaded grounds, river banks; elevation unknown; endemic to Trinidad.

SPECIMENS EXAMINED: TRINIDAD. St. Ann's Cascade, 23 Oct 1923, Broadway (BM, F); St. Ann, 28 Oct 1923, Broadway 5196 (F, G, MO); banks of the Oropucle River, 5-6 miles posts, via the Mora forest, 27 Sep 1931, Broadway 7749 (K). ST. GEORGE CO.: Government house, 18 Nov 1907, Broadway 1934 (B-n.v., BM, BR, G, MO, NY, US, type coll. of S. broadwayi); Botanic Gardens, 18 Oct 1921, Broadway (BM, F, MO); Botanic Gardens, St. Ann's wild, 21 Oct 1931, Broadway 7897 (K, Z).

TAXONOMIC DISCUSSION: Selaginella broadwayi is very closely related to and is difficult to separate from S. minima. In S. broadwayi, megaspores examined

tend to have white reticulations over a marguerite to primrose yellow (lemon-yellow) background or are totally marguerite to primrose yellow, not white as in S. minima. Apparently, in S. broadwayi the white reticulations become abraded with time leaving only the marguerite to primrose yellow background of the exospore. Microspores of S. broadwayi have smooth, gemmate to clavate projections over a rugose microstructure, whereas those of S. minima have verrucate to gemmate projections covered with micro-echini, over a echinulate microstructure on both faces. In addition, the ventral sporophylls in S. broadwayi are characteristically completely hyaline, and morphologically smaller and narrower than the upper sporophylls, whereas those of S. minima are pale green, and morphologically mostly similar to or only slightly smaller than the upper sporophylls.

Selaginella broadwayi is also similar in size to S. simplex, and in Trinidad, where the two overlap, they have been confused. Selaginella broadwayi differs from the latter by the median leaves ovate to ovate-lanceolate (vs. lanceolate to lance-ovate) with an asymmetric (vs. rounded) base, and the acuminate or aristate apex  $\frac{1}{4}$  or less (vs.  $\frac{1}{2}$  or more) the length of the lamina. In addition, the distal face of the megaspores in S. broadwayi usually has reticulations composed of white ridges, whereas the distal face of the megaspores in S. simplex is entirely pinard yellow.

**3. *Selaginella simplex* Baker, J. Bot. 23: 293. 1885. (Figs. 5E-H).**

Type: BRAZIL. PARÁ: near Santarém, Jun 1850, Spruce 947 (Holotype: K!; isotypes: BM!, CGE-n.v., W!)

Plants terrestrial or epipetric. Stems ascending to suberect, stramineous to greenish, 0.6-5 cm long, 0.1-0.26 mm diam., not articulate, not flagelliform, not stoloniferous, 1- (2-) branched. Rhizophores axillary, restricted to the basal  $\frac{1}{3}$  of the stem, filiform, 0.04-0.14 mm diam. Leaves dimorphic throughout, thin-membranous, the upper surface green, composed of rounded cells with sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant, perpendicular to the stem, broadly ovate to ovate-elliptic,  $1.3-1.6 \times 0.8-1.0$  mm; base rounded, the acroscopic base not to weakly overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin greenish, shortly ciliate along basal  $\frac{1}{4}$  to  $\frac{1}{2}$ , serrulate apically, the basiscopic margin greenish, entire to serrulate; apex acute to acuminate, dentate at tip; the upper surface glabrous, without idioblasts or conspicuous stomata, the lower surface glabrous, without conspicuous idioblasts or stomata. Median leaves distant, ascending, lanceolate to lance-ovate,  $0.6-1.2 \times 0.18-0.36$  mm; base rounded; margins greenish, serrate to serrulate; apex long-acuminate to aristate, the acumen or arista  $\frac{1}{3}$  to  $\frac{1}{2}$  the length of the lamina, 0.16-0.3 mm, dentate at tip; both surfaces glabrous, without conspicuous idioblasts or stomata. Axillary leaves similar to lateral leaves. Strobili terminal on branch tips and main stem apex, lax,

flattened, and dorsiventral, 1.8-6.4 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along ca.  $\frac{1}{2}$  to  $\frac{3}{4}$  the sporophyll length, asymmetric to lanceolate, 1.28-1.66  $\times$  0.4-0.78 mm, with a strongly developed denticulate keel along midrib, the base rounded, the margins greenish, serrate to shortly ciliate, the apex acuminate to mucronate, the upper surface green, composed of rounded cells with sinuate walls, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts or conspicuous stomata, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls; ventral sporophylls almost colorless to completely hyaline, ascending, without an adaxial flap, ovate-lanceolate to lanceolate, 0.96-1.34  $\times$  0.36-0.46 mm, with a well developed denticulate keel along midrib, the base rounded, the margins greenish, short- to long-ciliate along basal  $\frac{1}{2}$ , serrate apically, the apex long-acuminate to moderately long-aristate, both surfaces made of elongate, hyaline cells with sinuate walls, glabrous, without conspicuous idioblasts or stomata. Megasporangia in two ventral rows; megaspores pinard yellow, frequently with an equatorial flange, the proximal face granulose-tuberculate or rugulate, the distal face reticulate with open to close reticulum of low ridges, 260-300  $\mu$ m diam. Microsporangia usually in two dorsal rows or absent from dorsal rows, if absent then dorsal sporophylls sterile; microspores not studied.

**HABITAT AND DISTRIBUTION:** On dry and open river banks, on banks in

hillside savannas, wet ravines on shaded and wet rock ledges in Cerrado vegetation; 700-1200 m; Mexico, Costa Rica, Venezuela, Trinidad, Brazil, and Bolivia.

SPECIMENS EXAMINED: MEXICO: NAYARIT: 3 km W of Mazatán, 900 m, 20 Nov 1963, Feddema 2660 (MICH). OAXACA: 3 km N of Matías Romero, 17 Dec 1972, R. Tryon & A. Tryon 7389 (GH p.p.); Putla, 8 km N of Putla, 2000' [610 m], 11 Oct 1969, Mickel & Hellwig 3996a (NY).

COSTA RICA. ALAJUELA: Banks of Río Rosales, Grecia, 850 m, 8 Dec 1933, Brenes 1806 [sometimes labelled as Valerio 2086 or 1806] (CR,US-2 sheets), carretera Alajuela-Grecia, orillas del Río Rosales, 850 m, 8 Dec 1933, Brenes 17494 (F, NY), Brenes 18159 (CR); 10 Dec 1933, Brenes 18832 (NY); 13.2 km W de Alajuela en la carretera Alajuela-Grecia, Río Rosales, ca. 100 m detrás de la fábrica de Mosaicos "El Río," 11 Dec 1991, Valdespino 1290 (CR, NY, PMA); Río Rosales, Grecia, 850 m, 8 Dec 1933, Valerio 2083 (BM).

VENEZUELA. CARABOBO: La Mona, near Chirgua, 700 m, 1 Jan 1939, Alston 5929 (BM, US).

TRINIDAD. Maracas, bottom part of road to the waterfall, 25 Feb 1927, Broadway 6581 (BM, F, G, K, S, Z), road to the falls, 14 Oct 1927, Broadway 6697 (F, K); 14 Oct 1927, Homersley s.n. (BM).

BRAZIL. GOIÁS: Serra dos Cristais, 5 km E of Cristalina, ca. 1200 m, 5 Apr 1973, Anderson 8187 (MICH, NY), ca. 8 km S of Cristalina, 17°S, 48°W, 1200



m, 6 Mar 1966, Irwin et al. 13654 (NY); region of the Chapada dos Veadeiros, Campo Sujo, 21 km N of São João da Aliança, 14°30'S, 47°30'W, 20 Apr 1956, Dawson 14482 (LAM, US). PARÁ: near Santarém, Spruce 569 (M), near Santarém, Spruce 947 (BM, K, type coll. of S. simplex). PERNAMBUCO: Tapéra, 8 Oct 1931, Pickel 2812 (BM, US). WITHOUT SPECIFIC STATE OR LOCALITY: Burchell 7006 (K p.p.).

BOLIVIA. SANTA CRUZ: near Santa Cruz, 25 Apr 1902, Williams 2657 (NY, US-2 sheets).

TAXONOMIC DISCUSSION: Selaginella simplex is very similar in size and general morphology to S. minima, and in the past they have been very much confused (Valdespino, 1993b). It can be distinguished from S. minima by the characters given in the key, most noticeably by having greenish (vs. hyaline) leaf and sporophyll margins, the upper surface of lateral leaves and sporophylls without (vs. frequently with) conspicuous stomata and short hairs, yellow (not white) megaspores, with the proximal face granulate-tuberculate (not striate, reticulate, or rugulate).

**4. *Selaginella correae* Valdespino, Brittonia 45: 315. 1993. (Map 1).**

Type: PANAMA. CHIRIQUÍ: Bugaba, Represa de Fortuna, ca. 18 km N de los Planes de Hornito, entrada a Quebrada Honda ca. 200 m N del puente sobre el embalse, 1.2 km W de la entrada, 1100-1200 m, 3 Jan 1992, Valdespino, Ríos-Lewy, Young & Chacón 1335 (Holotype: PMA!; isotypes: CR!, MO!, NY!, UC!, US!).

Illustration: Valdespino, 1993b (Figs. 1A-F; 2A-D.).

Plants epipetric or terrestrial, minute, moss-like. Stems creeping, greenish, 1-4 cm long, 0.09-0.14 mm diam., not articulate, 1-branched. Rhizophores axillary, borne throughout the stem, filiform, 0.03-0.07 mm diam. Leaves dimorphic throughout, thin-membranous, iridescent, the upper surface bluish green, composed of rounded cells with sinuate walls, the lower surface silvery green, composed on elongate cells with sinuate walls. Lateral leaves distant or imbricate, mostly perpendicular to the stem, ovate to ovate-elliptic,  $1.2-2.3 \times 0.65-1.3$  mm, the acroscopic base rounded, slightly overlapping the stem, the basiscopic base oblique to rounded, not overlapping the stem; margins greenish, the acroscopic margin serrate, the basiscopic margin entire near base, sparsely serrate to strongly serrate apically; apex acute to narrowly obtuse, dentate at tip; upper surface hispid, without idioblasts; lower surface glabrous with obscure idioblasts. Median leaves distant, ascending, elliptic to ovate-elliptic,  $(0.6-)1-1.45 \times (0.2-)0.32-0.48-(0.6)$  mm, the inner base oblique, the outer base rounded; margins hyaline, serrate; apex

long-aristate, the arista to half of lamina length, 0.3-0.7 mm, dentate at tip and edges; both surfaces glabrous, without conspicuous idioblasts. Axillary leaves, when present, similar to lateral ones. Strobili terminal or borne throughout stem, lax, flattened, and dorsiventral, 1.25-3(-3.5) mm. Sporophylls dimorphic; dorsal sporophylls blue-green to green, spreading, basally attached to the axis, with an adaxial flap extending along  $\frac{1}{2}$  to  $\frac{2}{3}$  the sporophyll length, lanceolate to asymmetric, 1-1.5 × 0.37-0.65 mm, with a strongly developed ciliate-denticulate keel along midrib, the base ± rounded, the margins hyaline, serrate, the apex long-acuminate to shortly aristate, the upper surface green, composed of ± rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without conspicuous idioblasts, with stomata along midrib; ventral sporophylls almost colorless to completely hyaline, ascending, pseudopeltately attached to the axis, without an adaxial laminal flap, ovate-elliptic or ovate-lanceolate, 1.2-1.4 × 0.5-0.6 mm, with a slightly developed ciliate-denticulate keel along midrib, the base rounded to slightly cuneate, the margins obscurely hyaline or greenish, serrate, the apex long-acuminate to short-aristate; both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts and stomata. Megasporangia in two ventral rows, infrequently some dorsal; megaspores whitish, with or without a slightly developed equatorial flange, the proximal face reticulate with close reticulum of low ridges, the distal face reticulate with open reticulum of rather low ridges, 230-260 μm diam. Microsporangia in two dorsal rows, infrequently some

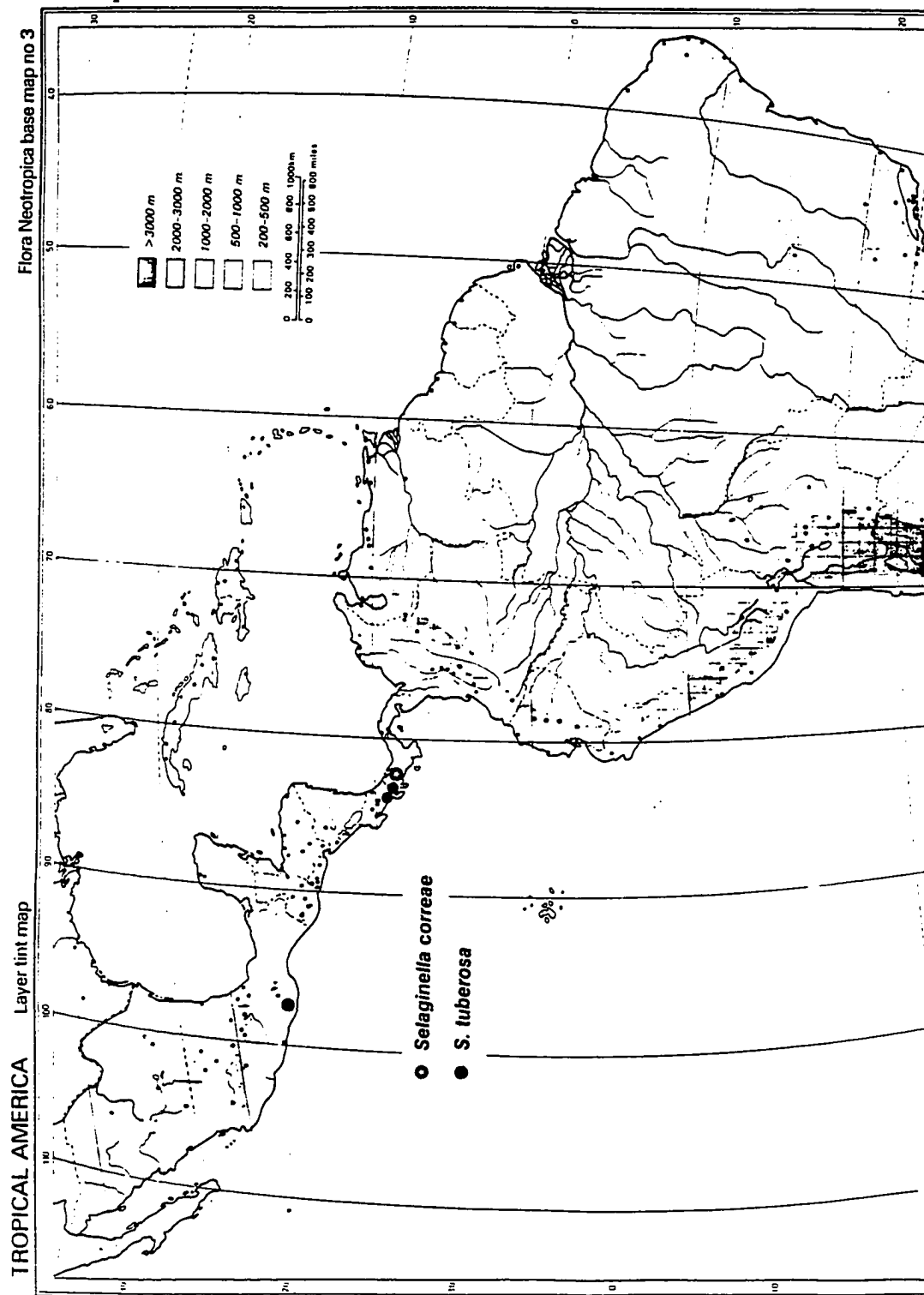
ventral; microspores tan to orange, without an equatorial flange, the proximal and distal faces seemingly smooth, 25-40  $\mu\text{m}$  diam.

HABITAT AND DISTRIBUTION: On rocks or soil on steep forested slopes; 1100-1200 m; known only from the Fortuna region of Chiriquí in Panama.

SPECIMENS EXAMINED: PANAMA. CHIRIQUÍ: Bugaba, Represa de Fortuna, ca. 200 m NW del puente sobre el embalse, 13 Jan 1989, Valdespino et al. 968a (NY, PMA).

TAXONOMIC DISCUSSION: Selaginella correae is morphologically interesting because it often bears strobili throughout the stem, due to the continued vegetative growth of the strobilus tip. In Central America, S. correae is most similar to and likely to be confused with S. minima Spring and S. simplex Baker, with which it shares small size, bluish green iridescent upper leaf surface, lax, flattened and dorsiventral strobili, dimorphic sporophylls, and a laminal flap on the dorsal sporophylls (Valdespino, 1993b). They can be distinguished, however, by the characters given in the key.

Map 1.



**5. *Selaginella hyalogramma* Valdespino sp. nov. (Figs. 2A-H; 6E-H; Map 2).**

Type: VENEZUELA. TÁCHIRA: Dist. Córdoba, Cerro La Camiri, S of the town of Río Negro, 7°36'N, 72°10'W, 430-530 m, 6 Nov 1982, Davidse & González 21525 (Holotype: MO!; isotype: UC!).

S. muscosae Spring affinis sed foliis intermediis basi asymmetricis, apice acuminatis diversa.

Etymology--Gr., hyalinus, glassy, transparent, and gramme, line; referring to having hyaline idioblasts on the upper surface of lateral and median leaves, and sporophylls, and on the lower surface of lateral leaves.

Plants epipetric. Stems ascending to suberect, stramineous to greenish, 4-7 cm long, 0.4-0.6 mm diam., not articulate, not flagelliform, not stoloniferous, 2- or 3-branched. Rhizophores axillary, restricted to the basal  $\frac{1}{3}$  or  $\frac{1}{2}$  of the stem, filiform, 0.1-0.2 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of rounded cells with sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant, almost perpendicular to the stem, broadly ovate to broadly ovate-lanceolate, 2-2.5 × 1.0-1.5 mm; base rounded to semicordate, the acroscopic base strongly overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin weakly hyaline, serrate or shortly ciliate along basal  $\frac{1}{4}$  and serrulate

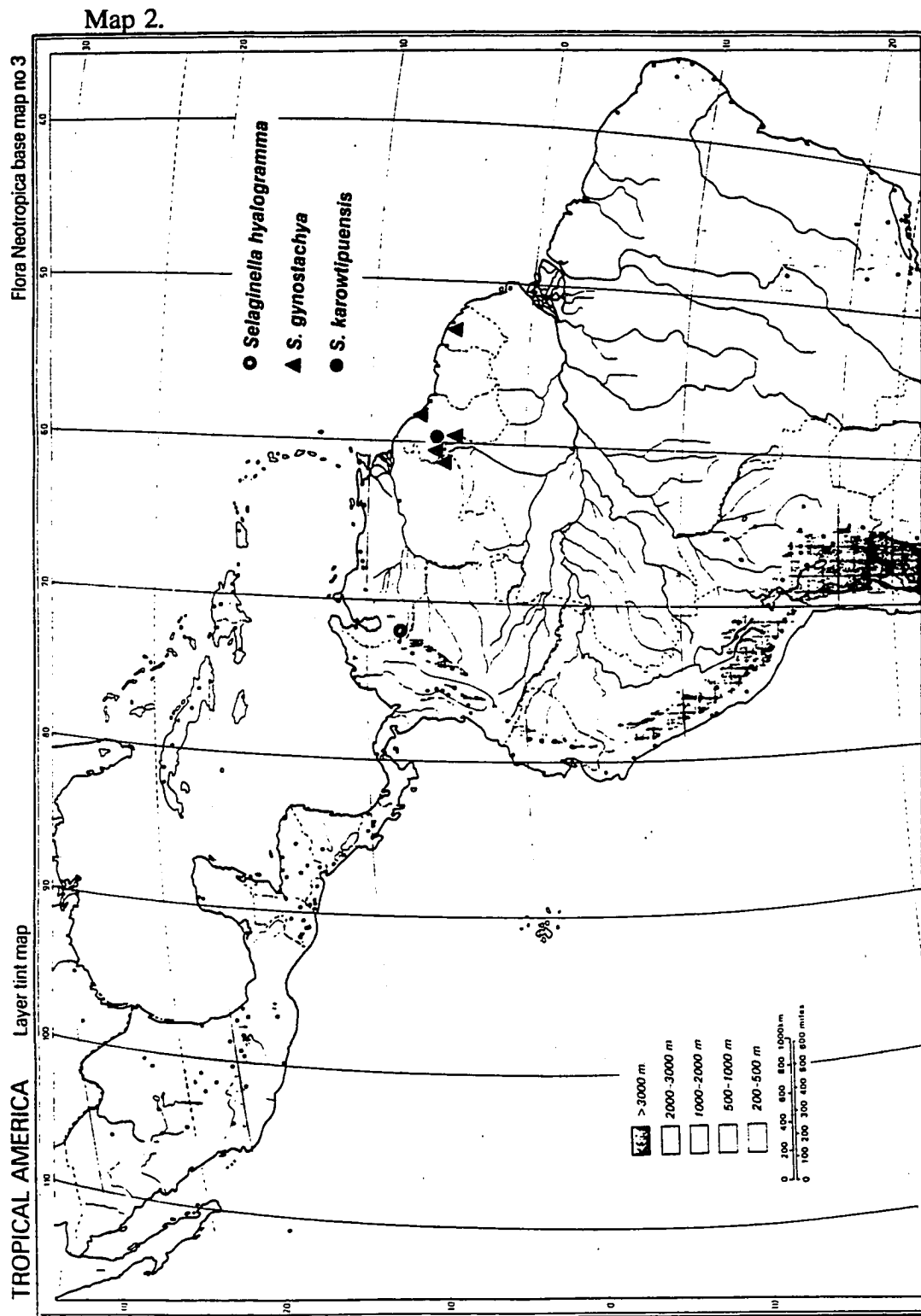
apically, the basiscopic margin weakly hyaline or pale green, serrulate; apex obtuse, dentate at tip; the upper surface with obscure short hairs near the basiscopic margin, with conspicuous idioblasts, the lower surface glabrous, with conspicuous idioblasts and with stomata along midrib. Median leaves distant, ascending, lanceolate,  $1.0-1.7 \times 0.5-0.7$  mm; base asymmetric, the inner base truncate, the outer base auricled; margins hyaline, serrate to serrulate; apex acuminate, the acumen  $\frac{1}{8}$  or less the length of the lamina, 0.1-0.2 mm long, dentate at tip; both surfaces glabrous, the upper surface with conspicuous idioblasts and stomata, the lower surface without conspicuous idioblasts or stomata. Axillary leaves similar to lateral leaves or more cordiform. Strobili terminal on branch tips and main stem apex, lax, flattened, and dorsiventral, 4-11 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along ca.  $\frac{1}{2}$  to  $\frac{3}{4}$  the sporophyll length, asymmetric to lanceolate,  $1.6-2.1 \times 0.5-0.9$  mm, with a strongly developed and slightly denticulate keel along midrib, the base rounded, the margins hyaline, serrate to serrulate, the apex acute to acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with conspicuous idioblasts and stomata, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls; ventral sporophylls almost colorless to completely hyaline, ascending, pseudopeltately attached to the axis, without an adaxial flap, ovate to broadly ovate,  $1.4-1.85 \times 0.6-0.72$  mm, with a well developed and slightly denticulate keel along midrib, the base

rounded, the margins hyaline, serrate, the apex long- to short-acuminate, both surfaces made of elongate and hyaline cells with sinuate walls, glabrous, with conspicuous idioblasts, and without conspicuous stomata. Megasporangia in two ventral rows; megaspores pinard- to baryta yellow, with a prominent equatorial flange, the proximal face reticulate with close reticulum of low ridges, the distal face reticulate with open reticulum of high ridges, 270-300  $\mu\text{m}$  diam. Microsporangia usually in two dorsal rows; microspores not studied in detail.

HABITAT AND DISTRIBUTION: On mossy sandstone on steep forested cliff with open landslide areas; 430-530 m; known only from the type collection in Venezuela.

TAXONOMIC DISCUSSION: Because of its idioblasts on the upper and lower surfaces of the leaves and sporophylls, and yellow megaspores, S. hyalogramma seems to be related to and can be confused with S. muscosa Spring. It differs from the latter by the median leaves with an asymmetric (vs. cordate to semicordate, or rounded) base, an acuminate (not long-aristate) apex, and by the distal face of the microspores smooth (vs. clavate). The smooth microspores of S. hyalogramma seem to relate it to the group formed by S. seemannii, S. gynostachya, and S. karowtipuensis.





6. *Selaginella muscosa* Spring in Martius, Fl. Bras. 1 (2): 120. 1840. (Figs. 6A-D; 9C & D).

Type: BRAZIL. SEBASTIÃO POLIS [RIO DE JANEIRO]: In silvis Macahé, locis udis, paludosis, Luschnath (Holotype: probably BR-herb Mart.-n.v.; probable isotypes: B-n.v. [fide Alston et al., 1981: 297.], M-n.v.).

Lycopodium brasiliense Raddi, Pl. Bras. Nov. Gen. 1: 82. 1825.

Type: BRAZIL. RIO DE JANEIRO: Raddi (Holotype: probably at PI; probable isotypes: BM!, BOLO-n.v., K!, FI-n.v., FI-negative 845!, photo NY! [for more details on Raddi's collections and types see Pichi-Sermolli and Bizzarri, 1992: 212-218.]).

Selaginella brasiliensis (Raddi) A. Braun, Ann. Sci. Nat. Bot. V, 3: 290. 1865.

Type: same as Lycopodium brasiliense Raddi.

Lycopodium pallidum Beyrich ex Gaudichaud in Freycinet, Voy. Uranie 285.

1828, nom. superfl. for L. brasiliense Raddi, hence illeg. and to be rej. under Article 52.1 of the ICBN (Greuter, 1994).

Lycopodium albidulum Swartz var. majus Greville & Hooker, Bot. Misc. 2: 399. 1831.

Type: BRAZIL. [SANTA CATARINA]: Macrae (Lectotype: K!, here designated; isoelectotypes: BM!, BR!, K!). Other syntypes: "PERU" [ECUADOR]. PICHINCHA: Jameson (K-n.v.?); BRAZIL. Raddi (BM!, K!).

Selaginella apus (Linnaeus) Spring var. tetragonostachya Spring in Martius, Fl.

Bras. 1 (2): 120. 1840.

Type: BRAZIL. SEBASTIANÓ POLIS [RIO DE JANEIRO]: Ad margines viarum inter Pedro Alvez et João Gomez, Pohl [3866] (Lectotype: W!, here designated; isoelectotypes: BR!, OXF!). Other syntypes: BRAZIL. SEBASTIANÓ POLIS [RIO DE JANEIRO]: Raddi (BM!, K!); in Calçada da Estrella, Gaudichaud (not located). BAHIA: In sylvis Catingas inter Cachoeira et Monte Santo, [Martius] (M!).

Selaginella polysperma Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 138. 1843.

Type: BRAZIL. RIO DE JANEIRO: Gardner (Holotype: LG!).

Selaginella beyrichii A. Braun, App. Ind. Sem. Hort. Berol. 13. 1857.

Type: No specimen cited (probably at B) [fide Alston et al., 1981: 297.].

Selaginella anocardia A. Braun, Ann. Sci. Nat. Bot. V, 3: 290. 1865.

Type: BRAZIL. RIO DE JANEIRO: 1859, Rudio (Lectotype: B!, here designated, photo BM!; isoelectotype: B!, BM!, M!). Other probable syntypes: BRAZIL. RIO DE JANEIRO: [Petrópolis?], Jelinek 209 (B-2 sheets!, W!). SÃO PAULO: Serra de Cubatas, 1855, Lindberg (B!).

Selaginella brevipes Fée, Crypt. Vasc. Brésil 226. 1869, nom. illeg., non A. Braun (1867).

Type: BRAZIL: RIO DE JANEIRO: Serre des Orgues [Serra dos Orgãos], 30 Apr 1868, Glaziou 2241 (Holotype: P!; isotypes: B!, BR!, P!).

Selaginella cunninghamii Baker, J. Bot. 22: 110. 1884, **syn. nov.**

Type: BRAZIL. RIO DE JANEIRO: [Corcovado, Lagoinha, 16 May 1873], Glaziou 7039 (Lectotype: K!, here designated; isoelectotypes: P!, S!). Other

syntypes: BRAZIL. RIO DE JANEIRO: 1867, Cunningham (K!); Rio de Janeiro, Glaziou 5217 (B!, BM!, K!, P!, S!).

Selaginella niederleinii Hieronymus, Bot. Jahrb. Syst. 22: 418. 1896.

Type: ARGENTINA. MISIONES: Paggi, Río Alto Uruguay, Aug 1887, Niederlein 630 [1252] (Holotype: B!; isotypes: K!, R!).

Selaginella feei Hieronymus in Engler & Prantl, Nat. Pflanzenfam. 1 (4): 713,

1901, nom. nov. for S. brevipes Fée (1869), non S. brevipes A. Braun (1867).

Type: same as S. brevipes Fée.

Selaginella brasiliensis (Raddi) A. Braun var. crassinervia Hieronymus ex

Bonaparte, Notes Ptérid. 2: 137. 1915, nom. nud.

Plants terrestrial or epipetric. Stems creeping, stramineous to greenish, 4-17 cm long, 0.3-0.65 mm diam., not articulate, not flagelliform, not stoloniferous, 2 or 3-branched. Rhizophores axillary or occasionally with both an axillary and a dorsal rhizophore, throughout or restricted to the basal ½ of the stem, filiform, 0.1-0.2 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of ± rounded cells with slightly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, almost perpendicular to the stem, broadly ovate to broadly ovate-oblong, 2-3.3 × 1.2-1.7 mm; base subcordate, the acroscopic base strongly overlapping the stem, the basiscopic not overlapping the stem; margins hyaline or

pale green, the acroscopic margin serrate or shortly ciliate along basal  $\frac{1}{4}$  and serrulate apically, the basiscopic margin serrulate; apex acute to shortly acuminate, dentate at tip; both surfaces glabrous, with conspicuous idioblasts, or the idioblasts present only on lower surface, and without conspicuous stomata. Median leaves distant, ascending, broadly-ovate to ovate-lanceolate,  $(0.86-1.16) \times 0.6-1.16$  mm; base asymmetric with the inner base truncate and the outer base weakly auricled, subcordate, or rounded; margins hyaline, shortly ciliate along basal  $\frac{3}{4}$ , serrate to serrulate along apical  $\frac{1}{4}$ ; apex long to short-acuminate to long-aristate, the acumen or arista  $\frac{1}{4}$  to  $\frac{1}{2}$  or more the length of the lamina,  $(0.32-0.5-0.9)$  mm long, puberulent and dentate at tip; both surfaces glabrous, the upper surface with conspicuous idioblasts or infrequently absent and without conspicuous stomata, the lower surface with obscure to conspicuous idioblasts, and without conspicuous stomata. Axillary leaves similar to lateral leaves or more cordiform, except the base frequently cordate. Strobili terminal on branch tips and main stem apex, lax, flattened, and dorsiventral,  $(3-5-15)$  mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along ca.  $\frac{1}{2}$  the sporophyll length, asymmetric or broadly ovate to broadly lanceolate,  $1.6-2.4 \times 0.6-1.08$  mm, with a strongly developed and slightly denticulate keel along midrib, the base rounded, the margins hyaline, shortly ciliate to serrate, the apex long-aristate, or short- to long-acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with or

without conspicuous idioblasts and stomata, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts or stomata; ventral sporophylls almost colorless to completely hyaline, ascending, peltately attached to the axis, with a slightly developed adaxial flap, broadly ovate,  $1.4-1.86(-2.1) \times 0.6-1$  mm, with a well developed and slightly denticulate keel along midrib, the base cordiform to rounded, the margins hyaline, shortly ciliate to serrate, the apex long-aristate, or long to short-acuminate, both surfaces made of elongate and hyaline cells with sinuate walls, glabrous, without conspicuous idioblasts or stomata. Megasporangia in two ventral rows; megaspores baryta yellow to empire yellow or white, with a strongly developed equatorial flange, the proximal face seemingly smooth to granular, or striate marginally, the distal face reticulate with open reticulum of high ridges, (280-)325-360  $\mu\text{m}$  diam. Microsporangia frequently abortive in two dorsal rows, or few mature near the apex on dorsal rows, or sometimes totally absent; microspores tan to orange, frequently with a weakly developed equatorial flange, the proximal face centrally rugose, smoother near the margins, or seemingly smooth throughout, the distal face clavate over a smooth microstructure, 18-30  $\mu\text{m}$  diam.

**HABITAT AND DISTRIBUTION:** On wet forested slopes, wet mossy rocks, river banks, and granitic rocks; 10-1600 m; Venezuela, Trinidad, Tobago, French Guiana, Peru [?], Brazil, Paraguay, Argentina, and Uruguay.

SPECIMENS EXAMINED: VENEZUELA: DELTA AMACURO: Imataca Mts., S of Santa Catalina, eastern end of Tortola Island, delta of Orinoco River, Nov 1896, Thompson 21 (US). SUCRE: Arismendi, Parque Nacional Península de Paria, vía El Olvido, 150 m, Jan 84, Fernández et al. 669 (UC).

TRINIDAD. CARONI: Aripo road, near 4 mi post, 24 Feb 1928, Broadway 6800 (BM-2 sheets, F, K, MO, S); Aripo road, at the bathing pool, Riverside, 3 Nov 1929, Broadway 7678 (BM, Z); Aripo road, near 2½ mi post, 10 Jan 1930, Broadway 7510 (BM, F, S); Heights of Aripo, 10-26 Jan 1922, Broadway 9984 (NY); Matchepoorie [Machapoone?], 11 Mar 1921, N. Britton & E. Britton 2232 (K, NY). ST. ANDREW: Oropuche road via Valencia, 13 Mar 1925, Broadway 5581 (K, MO); Oropuche River, 5-6 mi post, via the Mora forest, 27 Sep 1931, Broadway 7749 (BM, K); road leading to the Oropuche, 28 Feb 1932, Broadway 7923 (K). ST. GEORGE: along the Arima-Blanchisseuse Road, 9-23 Feb 1950, Howard 10381 (BM); Arouca, Five Rivers (Laurel Hill), 15 Feb 1928, Broadway 6810 (BM, F, K); Blanchisseuse, 12 May 1908, Broadway 2255 (BM, BR, K, MO, Z); Blanchisseuse, 15 May 1908, Broadway 3034 (BM); Blanchisseuse road, near 4 mi post, 26 Feb 1926, Broadway 5990 (BM, K, Z); Blanchisseuse road, Verdant Vale bathing pool, 16 May 1926, Broadway 6224 (BM, F, K, MO, S); Blanchisseuse road, St. Patrick state, near the river, 25 Oct 1931, Broadway 7898 (K); Blue Basin, Aug 1987, Hart 6531 (NY); Caura, 11 Jan 1929, Broadway 7046 (BM); Caura, 24 Jun 1934, Broadway (K); Grand Reviere, near the Shark River, N coast, 22 Oct 1932, Broadway 9131 (BM); Las Lapas, off the Blanchisseuse

road, 28 Oct 1927, Broadway 6757 (F, K, S); L'Orange road, Nov 13 1925, Broadway 5851 (BM, K); Maracas, near the Falls, 12 Mar 1926, Broadway 6022 (BM); Maracas, road to the bay, N near the top at "Geteau," 26 Jun 1929, Broadway 7281 (BM, F); Maracas, 14 Oct 1927, Homersley (BM); Maraval, 9 Dec 1928, Broadway 7055 (BM); Morne Bleu ridge from Texel station to Morne Bleu peak, 2400-2700 ft [732-823 m], 4 Jul 1984, Mickel 9490 (NY); North Post to Maqueripe, 22 Mar 1920, E. Britton et al. 922 (NY); Ortoire River, Guayaguayare road, 25 Mar 1921, N. Britton et al. 2549 (NY); Quaré River Valley, ca. 600 ft [183 m], 25 Jan 1931, Rodney (BM); Shark River forest, 23 Oct 1932, Broadway 9029 (BM, Z); St. Anne's wild, Botanic Gardens, 21 Oct 1931, Broadway 7897 (K); Santa Cruz Mts., 23 Dec 1907, Broadway 7030 (BM); Santa Cruz, 8 Jul 1927, Broadway 6654 (F, K); Santa Cruz, 8 Jul 1927, Broadway 6655 (F, K). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Mar 1897, Jenman s.n. (NY-3 sheets [one mixed with S. producta Baker]); 29 Jul 1927, Homersley 6¼ (BM); Matura mora forest, 1 Aug 1937, Sandwith 948 (BM, K).

TOBAGO. Back Hill, above Charlotteville, 7 Oct 1937, Sandwith 1661 (BM, K); Campbleton woods, Charlotteville, 19 Apr 1910, Broadway 3633 (BM, NY); Easterfield road between Mason Hall and Caledonia, 9-23 Feb 1950, Howard 10474 (BM); Forest Reserve above Caledonia, 7 Sep 1909, Broadway 3018 (BM, MO, S); Menna, 23 Mar 1914, Broadway 4839 (K, OXF); Moriah, 1 Dec 1920, Weiss (GH); NE from 5½ mi post on Roxborough-Parlatuvier road, 420 m, 19 Nov. 1974, Jermy 11270 (BM); The Widow, near Easterfield, Broadway 3514 (BM,



NY); s.d., Eggers 5781 (F).

FRENCH GUIANA. Montagnes de la Trinité, bassin de La Mana, 4°35'N, 53°21'W, 400 m, 18 Mar 1992, Cremers 12812 (BM, Z).

PERU. WITHOUT SPECIFIC DEPARTMENT OR LOCALITY: Hobb s.n. (BM) [perhaps a wrong locality!].

BRAZIL. BAHIA: Camacã, 10.6 km SW of Camacã on road to Jacareçí, right at bridge for 6.2 km to TeleBahia tower, 15°22'52"S, 39°34'11"W, 24 May 1994, Thomas et al. 10462 (NY); Palmeiras, Pai Inácio, BR242, W of Lençois at km 232, 12 Jun 1981, Boom & Mori 1161 (NY); s.d., Blanchet (K); s.d., Blanchet 2207 (G, W). CEARÁ: Baturité, Serra de Baturité, 1937-1938, J. Eugenio [Leite] 54 (MG p.p., RB p.p.); Baturité, Serra de Baturité, E of Morro do Ceu, 3 km da cidade de Baturité, 29 Jun 1939, J. Eugenio [Leite] 56 (RB p.p.); Baturité, Vidén (S. João), 14 Dec 1939, J. Eugenio [Leite] 1360 (RB). ESPÍRITO SANTO: Cachoeiro do Itapémirim, vargen Alta-Guimar, 23 Aug 1948, Brade 19346 (BM, RB); Entrada do Espírito Santo, Alto [Limocino?], 11 May 1946, Brade et al. 18129 (RB); Norte Rio Doce, Sep 1950, Vieira 103 (RB); Rio Mutum, Feb 1917, Luetzelburg 12925 (M); Serra do Caparaó, Santa Barvara do Caparaó, edge of stream affluent of Rio Caparaó, 21 Nov 1929, Chase 10075½ (BR, P, US). MINAS GERAIS: Caldas, 20 Sep 1873, Mosén 2022 (P, S-2 sheets); Caraça, 1500-1600 m, 5 May-5 Apr 1885, Vainio (herb. Vainio No. 33288) (GH); Christina, Aug 1912, Luederwaldt 20999 (BM); Fazenda de Santa Ana, s.d., s.c., herb. Saldanha 6472, 6473 (R); Fazenda de Santa Ana, Mar 1881, s.d., s.c., herb. Amelia (R); Juiz de

Fóra, 675 m, 20 Feb 1925, Chase 8558½ (US); cachoeira prope Juiz de Fóra, Jun 1902, Schwacke 14763 (RB); Mandiocas, [18°-19°S, 44°-45°W, 18 Oct 22 [1822?], Riedel (US); Olhos d' Agua, Damazio (RB); Ouro Preto, Serra de Itacolumy, 1936, Badini 318 (RB); Ouro Preto, 1931, Damazio (RB); Ouro Preto, 1932, Damazio (RB); Poços de Caldas, 30 Mar 1944, Delforge 49, 53 (RB); Rio Preto, Magalhães (herb. Silveira 158) (R); Sapé, s.d., Damazio 1880 [1800?] (RB); Serra de Antonio Pereira, near Ouro Preto, Nov 1900, Silveira 171 (R); Serra d' Agua Limpa, Feb 1881, s.c. herb. Amelia (R); Serra da Matuca, Mar 1901, Araujo (herb. Schwacke 14380) (RB); Serra do Babylonia, 2 Jul 1869, Glaziou 3543 (BR, P, S); Sêro, Serra de Monjolo, 18 km N of Sêro, 5 May 1945, L. O. Williams & Assis 6800 (GH); Sêro, Serra da Bocaina, 10 km NW of Sêro, 4 May 1945, L. O. Williams & Assis 6865 (GH). PARAÍBA-CEARÁ: Serra do Araripe, Luetzelburg 12538 (M). PARANÁ: Antonina, Reserva Biológica Sapitanduva, 50 m, 25 Oct 1989, Kramer & Hatschbach 10810 (F, Z); Cataratas do Iguaçu, 7 Oct 1989, Kramer 10602 (Z); Jaguariava, Rio Samambaia, 18 Nov 1970, Hatschbach & Guimarães 25466 (UC, US); Lucena, Wielewski 17 (S); Lucena, April 1904, Wielewski 72 (NY, UC); Lucena, 1905, Wielewski 72a (NY, UC); Morretes, Caiobá, Morro do Boi, 24 Apr 1981, Kummrow 1524 (UC); Rio Itambey, 8 Jul 1981, s.c. (Itaipú Binacional) 914 (MO); Serra do Mar, 580 m, 7 Jul 1914, Dusén 654a (S); Serra do Mar, Estação Marumbí, Estr. Ferro Curitiba-Paranaguá, 483 m, 25 Jan 1951, Tessmann 429 (RB); Serra Graciosa, 15 Dec 1879, Schwacke 2537 (R, RB). PERNAMBUCO: Cabo, Reserva de Gurjaú-Mata, s.d., Fonseca & Porto 8368 (MO)

p.p.); Ouipapá, Eugenio Brejinho, 15 Sep 1972, Andrade-Lima 72-7004 (F). **RIO DE JANEIRO:** Corcovado, 8 Sep 1867, Glaziou 1646 (BR, P); Corcovado, Lagoinha, 16 May 1873, Glaziou 7039 (K, P, S, syntype of S. cunninghamii Baker); Corcovado, 18 Jul 1927, Harshberger 895 (US); Corcovado, 15 Nov 1946, Hunnewell 18656 (MICH); Corcovado, 1 Jul 1873, Mosén 54 (S); 17 Jul 1873, Mosén 56 (S); Corcovado, 30 Sep 1874, Mosén 2735 (S); Corcovado, 10 Sep 1874, Mosén 2736 (S); Corcovado Mountain, Feb-Mar 1924, 800-1500 ft [244-525 m]; Corcovado, Murriel (NY); Corcovado, 10 Jul 1915, Rose & Russell 20186 (NY, US); Corcovado, 11 Jul 1915, Rose & Russell 20199 (NY, US); Corcovado, Jul 1915, Rose & Russell 21271 (US); Gavea, Jul 1889, Ule 270 = 2270 (P); Guanabara, Paineiras, 500 m, 26 May 1966, Beker 1 (R, US), 2 (K, P, R-2 sheets, US-2 sheets), 4 (R, US), 5 (R, US); Itatiaia, 1000 m, 24 Feb 1942, Brade 17189 (BM, G, MG, MO, RB); Itatiaia, Lote 17, 800 m, 12 Feb 1948, Brade 18850 (BM, RB); Itatiaia, Mar 1903, Hoehne 20996 p.p. (BM); Itatiaia, 26-30 Jul 1915, Rose & Russell 20441 (NY, US); Itatiaia, Moromba, SE side of Itatiaia Mt., Ribeirão Campo Belo, 150 km WNW of Rio de Janeiro, 1100 m, 31 Oct 1965, R. Tryon & A. Tryon 6623 (GH); Itatiaia, Moromba, SE side of Itatiaia Mt., Ribeirão Campo Belo, 150 km WNW of Rio de Janeiro, 1100 m, 31 Oct 1965, R. Tryon & A. Tryon 6654 (F, GH, UC); Itatiaia, 800 m, Jun 1913, Tamandaré 833 (RB); Mage, Cachoeiras do Macacu, Reserva Ecologica Estadual do Paraíso, 22°27'S, 42°5'W, 21 Nov 1991, Sylvestre et al. 667 (RB); Nitheroy, 25 Dec 1901, Dusén 147 (S); Nitheroy, 21 Jul 1873, Mosén 55 (S-2 sheets); Nova Friburgo, Jul 1946, J. Eugenio

Leite 4107 (F); Nova Friburgo, Teodoro de Oliveira, km 1 da Estrada para a área de segurança da EMHASA, 27 Mar 1989, Sylvestre et al. 145 (RB); Nova Friburgo, Teodoro de Oliveira, km 1 da Estrada para a área de segurança da EMHASA, 27 Mar 1989, Sylvestre et al. 151 (RB); Paineiras to Corcovado, 22°56'S, 43°14'W, 465-710 m, 17 Nov 1928, L. B. Smith 1263 (GH); Paraty, 8 Nov 1991, Marquete et al. 443 (RB); Paraty, Entrada da Rio Santos para Paraty, 1000 m, 8 May 1991, Sylvestre et al. 404 (RB); Petropolis, Jelinek 211 (W); [Petropolis?], s.d., Jelinek 212 (W); Organ Mts., 12 Aug 1915, Rose & Russell 20750 (NY, RB, US); Pico do Papagaio, Emygdio 386 (R); Pico da Tijuca, 10 Jun 1922, Freire (R); Rio Dauro, 13 Aug 1878, Saldanha & Glaziou 5006 (R); Santo Antônio de Imbé, Forquilhas, 600 m, 1932, Brade [Brade & Lima] 11663 (BM-2 sheets); Santo Antônio de Imbé, Apr 1932, Brade & Lima 11665 (GH, R); Santo Antônio de Imbé, Apr 1932, Brade & Lima 11666 (R); Serra d'Estrella, in humidis prope Novo Friburgo et humidis umbrosis montosis Corcovadensis, 1823, Beyrich [herb. Filic. Luerssen 7198] (P); Serra da Estrella, 700 m, 29 Oct 1946, Brade & Apparicio 18657 (RB); Serra da Estrella, Aug 1915, Luetzelburg 6071 (M); Serra do Itatiaia, km 3, 950 m, 30 Jun 1930, Brade 10270 (BM, R); Serra do Itatiaia, 800 m, 4-10 Jun 1913, Brade 6507 (BM, [Tamandaré & Brade 6507 at NY], S); Serra do Itatiaia, Estrada Monserrat ao Maromba, Nov 1925, Vaughan s.n. (BM, RB); Serra do Itatiaia, Mont Serrat, 900 m, 15 Jun 1930, Brade 10051 (BM, R); Serra do Itatiaia, Monte Serrat, 900 m, 21 Oct 1903, Dusén 2148 (P, R, S); Serra do Itatiaia, Moromba, Brade 10272 (R); Serra do Itatiaia, Sitio do Walter, Apr 1926,

Sampaio 4054 (R); Serra do Mar, 1886, Ule 271 (P); Serra dos Orgãos, Jan 1883, Schwacke (R); Serra dos Orgãos, s.d., Schwacke 4393 (RB); Serra dos Orgãos, Cascata Imbui, 17 Jul 1948, Rizzini 310 (RB); Serra dos Orgãos, Morro Assu, 1910, Luetzelberg 12980 (M); Serra dos Orgãos, Jun 1916, Luetzelberg 6673 (M p.p.); Serra dos Orgãos, road to Theresópolis [Teresópolis], ca. Soberbo, 968 m, 1 Jul 1966, Lourteig 1853 (P, R, US); Serra dos Orgãos, 800-1200 m, Jun 1895, Werner 858 (P); Theresópolis [Teresópolis], Cachoeira Teroz [Feroz], Fazenda do Dr. Carlos Fuinle, 900-1000 m, [30] Jan 1944, Lutz 2081 (BM); Theresópolis [Teresópolis], Fazenda Cumary á Cachoeira Feroz, Lutz 2081A (R); Theresópolis [Teresópolis], 2700-2800 ft [823-854 m], 30 Jan 1944, Lutz 2107 (BM); Teresópolis, 1 May 1917, Sampaio 2379 (R); Serra da Tijuca, Morro de Archer, 13 May 1929, Brade (R); Serra da Tijuca, 17 Apr 1931, Brade 10740 (R); Tijuca, 25 Oct 1938, Alston & Lutz 307 (BM); Tijuca, entre Tijuca de Bico [Pico?] de Papagayo, 9 Jun 1929, Brade (R); Tijuca, Aug 1932, Brade 11991 (R), s.d., Freire & Vidal (R), 26 Nov 1938, Lutz 1053 (BM), Jul 1930, Martins (US), Martins 37 (US), 3 Jul 1957, Rente et al. 359 (R), 1 Aug 1957, Strang 49 (R); 1929, Brade 21.298 (BM); 5 May 1929, Brade (R); 10 Aug 1930, Brade 10376 (R); 1863, Bunbury (BR); 1867, Cunningham (K, syntype of S. cunninghamii Baker); s.d., d'Orbigny (P); s.d., d'Orbigny 36 (BR-2 sheets, G); 2000 ft [610 m], 15 Nov 1943, De Vol 3036 (MICH); 1837, Gardner 66 (BM, K, OXF, W); 1837, Gardner 67 (BM, G, K, OXF, P, W); 1818, Gaudichaud 11 (P); 1822, Gaudichaud (G, K, P); 1833, Gaudichaud 132 (G-2 sheets); 1831-1833, Gaudichaud 133 (P); s.d., Glaziou 3543\*

[the P sheet says: M. Geraeas] (BR, P, S); Oct 1871, Glaziou 4487\* [the P sheet says: 10 Jan 1876] (K, P); Oct 1871, Glaziou 4497\* [one of the P sheets says: Nova Friburgo, 11 Mar 1870], (K, P-2 sheets); Oct 1871, Glaziou 4498 (K); [Rio de Janeiro], Glaziou 5217 (B, BM, K, P, S, syntype of S. cunninghamii Baker); s.d., Glaziou 7038 (K, S); 12 May 1881, Glaziou 13365 (P, US); 1913, Goebel (M); entre Queimado and Rio de Janeiro, 13 Oct 1878, Glaziou 9313 (BR, K, P, S); Rio de Janeiro, James (DS); prope Sebastianópolis, Langsdorff (BR, K); Horto Botanic, 7 Sep 1892, Lindman A.207 (US, S-2 sheets); s.d., Miers (K); 200 m, 9 Sep 1911, Osten 5571 (S); May 1911, Petelot (F); 1840, Regnell (US); 1841, Regnell 369 (S); s.d., Riedel s.n. (K, P); Oct 1822, Riedel (K); 1847, Rudio (M); 1869, Rudio (P); 1816-1821, Saint-Hilaire 162 (P); s.d., Tonssell 243 (S); s.d., Weddel 666 (P); 1843, Weddel 667 (G, P). RIO GRANDE DO SUL: 20 Feb 1893, Lindman A1153 (S); near Belém Novo, 20 km S of Porto Alegre, 13 Jul 1952, Beetle 1592 (US); Hamburgo, 22 Oct 1892, Lindman A517 (S-2 sheets); ad montem Ferrabraz prope Hamburgo, 2 Sep 1949, Rambo 43205 (BM); Parecí near Montenegro, 26 Nov 1950, Rambo 49235 (BM, GH, S, UC); vicinity of Porto Alegre, 1940, J. Eugenio [Leite] 88 (NY); Porto Alegre, Morro da Policia, 28 Nov 1901, Malme (S); Porto Alegre, 20 Jul 1949, Rambo 42647 T (BM); Río Pardo, Fazenda Soledade, Jürgens L5 (BM); Río Pardo, S<sup>a</sup>Sa. Boa Esperança, 1904, Jürgens 10 (UC); Venancio Ayres, Quinta Boa Esperança, s.d., Jürgens L10 (BM, R); São Leopoldo, Quinta S. Manoel, s.d., Dutra 75 (BM, R); São Leopoldo, Quinta S. Manoel, s.d., Dutra 1607 (BM); São Leopoldo, Quinta S. Manoel, s.d., Dutra

1613 (BM); São Leopoldo, 20 m, 2 Oct 1935, Herter 96481 (G-2 sheets, Z); São Leopoldo, Nov 1941, J. Eugenio [Leite] 410 (NY); Santa Cruz, Dutra 227 (BM, R); Santa Cruz, 4 Oct 1904, Jürgens L17 (S); Santa Cruz, Picadado, Serro Alegre, 80 m, 12 May 1905, Jürgens L38 (S); Santa Cruz, Rio Picade, 8 Jan 1905, Stier L25 (NY, S, UC); Soledade, Secca Velha, Feb 1905, Jürgens L27 (UC); Taquara, 7 Jan 1934, Dutra 668 (BM, R); 10 km S de Veranópolis, 16 Nov 1971, Lindeman & Irgang 8113 (U p.p.); Vila Manresa, near Porto Alegre, 5 Jul 1949, Rambo 42719 (BM). SANTA CATARINA: Araranguá, Serra da Pedra, 7 Dec 1943, Reitz C.270 (GH); Ilha de Santa Catharina, Itacorobi, 15 Sep 1946, Rohr 384 (RB), Rio Tavares, 6 Jun 1948, Rohr 1061 (RB); Insel St. Catharina, Aug 1886, Ule 204 (=2204) (P, syntype of S. brasiliensis var. crassinervia Hieron. ex Bonap.); Joinville, Jun 1883, Ule 4 (= 2004) (P, syntype of S. brasiliensis var. crassinervia Hieron. ex Bonap.); Joinville, Mar 1905, L. Müller s.n. (BM, K, R), Apr 1905, L. Müller 104 (M, MICH, P, S-2 sheets, UC, US, W-2 sheets), 1908, L. Müller 104 (NY), 1906, L. Müller s.n. (A, L, UC), 1906, L. Müller 104 (UC); Lagos, Spannagel A.1 (S); Lagos, May 1905, Spannagel 85 (BM, NY); Lagos, s.d., Spannagel 85A (NY); Lagos, s.d., Spannagel 85d (UC); Laranjeira-Gebrige, Jun 1885, Ule 130 (= 2130) (P); Orleães, 90 m, 14 Nov 1946, Reitz 1787 (RB); Riosinho Bom Retiro, 1000 m, 4 Dec 1948, Reitz 2787 (RB); Reserva Forestal dos Pilões, 240 m, Duarte & Falcao 3141 (RB); São Francisco, s.d., 1883, Ule (herb. Luerssen 11979) (P), 19 Aug 1883, Ule 47 (=2047) (P), Oct 1884, Ule 102 (= 2102) (P); Schreiner (BM, R-2 sheets); s.d., Ule 1883 (P); Jun 1883, Ule 130 (P).

**SÃO PAULO:** Apiahy, Puiggari (herb Schwacke 2381) (RB), (2384) (BM, R, RB); Campo Grande, Serra do Mar, 800 m, Nov 1913, Brade 6599 (BM); Campos do Jordão, Jan 1946, J. Eugenio Leite 3899 (A, BM); Cantareira, Hoehne 21027 (BM); Serra da Cantareira, 11 Jan 1914, Tamandaré & Brade 6598 (NY, S, UC); Caraguatatuba, 15 Jul 1953, Hoehne 4111 (K), 4113 (SPF, NY); from Cubasão to Teresópolis, Dec 1886, Ule 271 (= 2271) (P); Iguapé, Morro das Pedras, Jul 1916, Brade 7690 (BM, NY, S), 10 Sep 1917, Brade 7691 (S), 1924, Brade 15719 (BM); Santos, José Menino, 26 Jun 1935, Hoehne 33427 (BM); Santos, 20 Dec 1874, Mosén 3125 (BR, K, M, O, R, S-2 sheets); Santos, 2 Sep 1965, Pedersen 7453 (MO); São José do Barreiro, Reserva Forestal da Bocaina, 1100-1300 m, Sucre et al. 2837 (RB). **WITHOUT SPECIFIC STATE:** 22 Mar 26 [1826?], Burchell (K); Burchell 1181 (K); Burchell 2392 (GH, K, L, NY, W); Burchell 2518 (K); Burchell 3168 (GH, NY, K); s.d., d'Orbigny 20 (LG); Gruta da Imprensa, 4 Nov 1945, Duarte 6 (R); Glaziou 4492 (P); 1886, King et al. (US); s.d., Langsdorf 23 (US); Langsdorf 26 (US); s.d., Miller (BM); 1861, Paul (MO); s.d., Raben 51 (BR); 1874, Richardson (BM); s.d., Riedel 87 (US); s.d., Riedel 88 (US); s.d., Sellow (K, L).

**PARAGUAY.** Cordillera de Mbatobi, Apr 1881, Balansa 3290 (K, L, P, US); Villa Encarnación, 28 Sep 1915, Rojas (herb. Osten 7870) (S).

**ARGENTINA. BUENOS AIRES:** Punta Lara (La Plata), 10 Jan 1929, Burkart 3186 (GH); Delta del Paraná, Jan 1931, Burkart 3711 (GH), near Recreo Naon, Paraná de las Palmas, 10 m, 28 Nov 1938, Goodspeed et al. 23260 (GH, UC).

**MISIONES:** Catar [Cataratas?], Iguazú, 100 m, Jul 1929, Borman s.n. (herb. Herter



85109 (G, NY, Z); Cataratas del Iguazú, 1 Sep 1949, Job (GH p.p.); Iguazú, 9 Sep 1915, Osten 7251 (S-2 shets); Loreto, Arroyo Yaberirí, Jul 1927, Burkart 1527 (GH); Parque Nacional Iguazú, 18 Jun 1982, Sharpe & Herrera 406 (NY); Parque Nacional Iguazú, 18 Jun 1982, Sharpe & Herrera 407 (NY); Puerto Aguirre near Iguazú, 15 Sep 1915, Rojas (herb. Osten 7252) (S); San Javier, 31 Jan 1926, Parodi 7058 (W).

URUGUAY. San Gabriel, Courbon s.n (P).

NOMENCLATURAL COMMENTS: It is possible that an earlier name for this species is S. crassinervia (Desvaux) Spring. The basionym Lycopodium crassinervium Desvaux, Mém. Soc. Linn. Paris 6: 190. 1827, was published without citation of any collection. In describing this species Desvaux indicated that the midrib was dark-colored due to a fungal disease. The species name was later transferred to Selaginella by Spring in 1840, in the same treatment in which he described S. muscosa. Braun (1865) synonymized S. crassinervia under S. brasiliensis (Raddi) A. Braun, and Alston (1934b) synonymized it under S. muscosa. Alston based his rejection of the epithet "crassinervia" on Article 51 of the International Rules of Botanical Nomenclature (Alston, 1934b), adducing that it was based on a diseased state. This Article was deleted (as Article 71) by the Leningrad Congress in 1975, and is no longer included in the current code (Greuter, 1994). Alston's rejection of the epithet "crassinervia," therefore, no longer applies. If it could be demonstrated that the type of L. crassinervium were

conspecific with S. muscosa, then the correct name for the resulting taxon would be S. crassinervia (Desvaux) Spring, since it has priority over S. muscosa. Among the specimens of S. muscosa that I received on loan from P, I found no specimen bearing any indication that it had been used by Desvaux to describe L. crassinervium. I conclude that it is advisable, at the present time, not to use the name S. crassinervia, because of the uncertainty about its correct application. A final decision must await a thorough search at P for original material of L. crassinervium studied by Desvaux.

Selaginella deltoides A. Braun and S. trifurcata Baker were synonymized by Alston et al. (1981) under S. muscosa. I have examined the types of S. deltoides [Syntypes: Spruce 2532 (B-n.v., BM!, BR!, CGE-n.v., GH!, K!, OXF!, P!, W!), Spruce 2535 (B-n.v., BM!, K! [2535 at G! = S. dendricola Jenman])] and of S. trifurcata [Spruce 2532 (B-n.v., BM!, BR!, CGE-n.v., GH!, K!, OXF!, P!, W!)], and concluded that they are conspecific, but belong to a different taxon from S. muscosa, and therefore are excluded as synonyms of the latter. Selaginella deltoides is allied to S. brevifolia Baker and S. sandwithii Alston. These three species are not considered members of subg. Heterostachys.

TAXONOMIC DISCUSSION: There seems to be an incipient racial differentiation between specimens from the northern part of the range (i.e., Trinidad and Tobago, and Delta Amacuro in Venezuela), which in general are found at (0-)150-800 m, the middle part of the range (e.g., Rio de Janeiro and São

Paulo), which are generally found at (200-)500-1300(-1600) and represent the typical form, and the southern part of the range (i.e., Rio Grande do Sul, Santa Catarina, Argentina, Paraguay, and Uruguay), which are found at (0-)10-100 m.

Specimens from the northern part of the range differ from typical S. muscosa by their more delicate, thinner leaves, the median leaves with a more oblique base, and stomata present along the upper surface of the outer base. Chromosome counts of this population were made from Trinidad specimens by Jermy et al. (1967). The authors, however, misidentified these specimens and reported the chromosome counts under three different names: S. hartii Hieron., (Jermy 2102, K!),  $2n = 18$ ; S. cladorrhizans A. Braun (Jermy 2559, K!),  $2n = 20$ ; and S. trifurcata Baker (Jermy 3119, K!),  $2n = 20$ . Nevertheless, this variation in chromosome number is significant and suggests different ploidy levels in this species. This may be as a result of apogamy, which has been documented for this species, as S. anocardia (= S. muscosa), by Goebel (1915, fide Ruf, 1976) and Geiger (1934, fide Ruf, 1976). Plants with strobili bearing only megasporangia are frequently found, which indicates that apogamy may be widespread in natural populations. It is also possible that the variation found in the ploidy level may be due to hybridization between typical S. muscosa and S. tenella (syn.: S. cladorrhizans) [which also has idioblasts on the upper surface of leaves and lateral leaves with oblique base], a common species in Trinidad, Tobago, and Venezuela, with which specimens from this population have been confused in the past. Alternatively, it could be the result of an error in the counts. In any case, these

hypotheses need to be tested by conducting detailed cytological studies involving both populations. Moreover, SEM study of microspores of both populations shows no variation in sculpturing pattern among them. Therefore, I prefer to treat the populations from Trinidad, Tobago, and Venezuela within S. muscosa.

Specimens from the southern part of the range are characterized by frequently lacking idioblasts on the upper surface of leaves, mostly oblong to oblong-ovate lateral leaves, median leaves with a shorter arista, and megaspores less reticulate. Leaf clearings made from specimens of this region show that idioblasts are present between the mesophyll and the lower surface, not in the upper epidermis. It was also observed that some were infected with a fungal disease along the midrib (e.g., Stier L.25, Jürgens L. 17), a condition frequently associated with typical S. muscosa, and particularly mentioned in the description of L. crassinervium (= S. crassinervia). In addition, SEM micrographs of microspores taken from specimens representing this population were identical to those of microspores taken from typical material from Rio de Janeiro (see also Morbelli, 1977). Therefore, I conclude they represent the same species, but probably an environmental form associated with drier habitats.

Some specimens under Glaziou's collection series marked here with an asterisk had labels with conflicting locality and date information among "duplicates of the presumed same collection". Wurdack (1970) has already commented on this matter, and concluded that such discrepancy was the result of Glaziou's deliberate tampering with the labels.

Alston et al. (1981: 298) reported S. muscosa as occurring in Colombia. I have examined almost all the specimens they cited for this country, except Garcia-Barriga 14948 (COL), and concluded that they represent several unrelated species, but not S. muscosa. These specimens have been newly determined as follows: Schultes & Cabrera 13931 (COL, GH, US) and Schultes & Cabrera 19268 (GH, US) = S. deltoides (see nomenclatural comments), Little & Little 9583 (COL) = S. flagellata, Foster & Smith 1392 (A, COL) = S. moritziana var. pearcei, and Alston 8486 (BM) mostly S. porelloides, plus S. revoluta Baker.

**7. *Selaginella porelloides* (Lamarck) Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 141. 1843.**

*Lycopodium porelloides* Lamarck, Encycl. 3: 652. 1791.

Type: Croît dans les Antilles [ex Insulis Caribensis] (Holotype: P-herb Lam.-n.v., Microfiche IDC 6207.750: II. 5. NY!).

*Stachygynandrum porelloides* (Lamarck) P. Beauvois, Prodr. Aethog. 110. 1805.

Type: Same as above.

*Lycopodium anomalum* Hooker & Greville, Bot. Misc. 2: 400. 1831.

Type: GUYANA. Demerara, Ankers (Holotype: K-n.v.).

*Selaginella anomala* (Hooker & Greville) Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 232. 1843.

Type: Same as above.

*Selaginella platyphylla* Baker, J. Bot. 23: 294. 1885, nom. illeg., non Veitch (1882).

Type: GUYANA. Demerara, Kaieteur ravine, Nov [18]78, im Thurn (Holotype: K!, fragment B!, fragment NY!).

*Selaginella platyphylla* Baker var. laxa Jenman, Ferns Brit. W. Ind. 389. 1909.

Type: GUYANA. [Kaieteur Falls region], Jenman 1819 (Holotype: K!).

*Selaginella jenmanii* Baker, Fern Allies 45. 1887.

Type. GUYANA. foot of the Kaieteur [Falls], Jenman 1480 (Holotype: K!, fragment BM!; isotypes: B!, E!, NY!).

*Selaginella leprieurii* Hieronymus, Hedwigia 43: 48. 1904, **syn. nov.**

Syntypes: FRENCH GUIANA. Apr 1845 Leprieur 168 (B?-n.v., BM!); Jun

1837, Leprieur 165 (B p.p.-n.v., K!, P!, US!).

Plants terrestrial or less frequently epipetric. Stems ascending to slightly erect, or sometimes slightly creeping, stramineous to greenish, 4-10 cm long, 0.1-1 mm diam, not articulate, not flagelliform, not stoloniferous, 1- or -2 branched. Rhizophores axillary-ventral or sometimes dorsal or ventral at lower stem base, restricted to basal  $\frac{1}{3}$  or  $\frac{1}{2}$  of the stem, 0.2-0.5 mm diam. Leaves dimorphic throughout, membranous, upper surface green, composed of rounded cells with sinuate walls, the lower surface silvery to silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves perpendicular to the stem, semicordiform to cordiform, (2-)2.5-4.3  $\times$  1-2.35 mm; base cordate to subcordate, the acroscopic base overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin hyaline, serrate to shortly ciliate on basal  $\frac{1}{2}$ , serrulate to entire apically, the basiscopic margin greenish, serrulate to entire; apex obtuse to slightly acute, dentate at tip, the upper surface glabrous or with short hairs near the basiscopic margin, without idioblasts, lower surface glabrous, with conspicuous idioblasts. Median leaves imbricate (especially in plants from sunny places) or distant, ascending, cordiform to ovate-deltate, 1.5-2.1  $\times$  0.75-2 mm; base cordate to subcordate with two slightly developed auricles or less frequently rounded; margins hyaline, serrate; apex short- to long-acuminate, or less frequently short-aristate, the acumen or arista  $\frac{1}{4}$  or less the length of the lamina, 0.3-0.56 mm long, dentate at tip; both surfaces glabrous, without conspicuous

idioblasts; the upper surface with conspicuous stomata scattered throughout the surface, the lower surface without stomata. Axillary leaves similar to lateral leaves or ovate-cordiform. Strobili terminal on branch tips and occasionally also on the stem tip, lax, flattened, and dorsiventral, sometimes branching at tip, 0.5-3.5(-6.5) cm long. Sporophylls dimorphic, basally attached to the axis; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along  $\frac{1}{2}$  to  $\frac{2}{3}$  the sporophyll length, ovate to ovate-lanceolate, or asymmetric,  $2-2.7 \times 1.0-1.3$  mm, with a strongly developed and denticulate keel along midrib, the base rounded, the margins hyaline, serrulate, the apex acute to shortly acuminate, the upper surface composed of  $\pm$  rounded cells with sinuate or straight walls, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without conspicuous idioblasts, with conspicuous stomata throughout green portion, the lower surface silvery, composed of elongate cells with sinuate walls, glabrous, with conspicuous idioblasts, without stomata; ventral sporophylls ascending almost colorless to pale green, ascending, without a laminar flap, broadly ovate to ovate-lanceolate,  $1.7-2.2 \times 1.0-1.2$  mm, with a slightly developed and sparsely dentate keel, the base rounded, the margins hyaline, serrate, the apex acuminate; the upper and lower surface silvery, composed of elongate cells with sinuate walls, glabrous, with conspicuous idioblasts only on the upper surface, without conspicuous stomata. Megasporangia occupying either the whole strobilus or only the the lower sporophylls; megaspores white, infrequently yellow, with a well developed equatorial flange, the proximal



face striate-reticulate to reticulate with open reticulum of high ridges, the distal face reticulate with open reticulum of high ridges, (230-)260-300(-350)  $\mu\text{m}$  diam; microsporangia frequently abortive or absent, the two rows of dorsal sporophylls lacking any sporangia, or infrequently present on dorsal sporophylls; microspores not seen.

HABITAT AND DISTRIBUTION: Exposed on road cuts, on stream banks, waterfalls, dripping rock faces, and sandstone tallus slopes in tropical rain forest or cloud forest; (0-)400-900 m; Costa Rica, Panama, Guadeloupe, Colombia, Venezuela, Trinidad, Guyana, French Guiana, Ecuador, and Brazil.

SPECIMENS EXAMINED: COSTA RICA. COCOS ISLAND: 1838, Barclay 2210 (BM); Sep 3 1967, Klawe (US); Chatam Bay, Mar 1964, Fournier 324 (NY); región de Bahía Yglesias, 0-50 m, Feb 1976, Gómez 6556 (CR), 6563 (CR); trail between Chatham and Wafer Bays, 100-232 m, Dec 1981, Gómez 18059 (CR-2 sheets), 18079 (CR), 18084 (CR-2 sheets); Wafer Bay, 100 m, 13 Apr 1965, Jiménez 3180 (F). HEREDIA: Cerro Sardinal, 2-2.5 km N of Chilamate de Sarapiquí (Finca La Martita), 10°28'N, 84°4'W, 80-160 m, 21 Jan 1986, A. R. Smith et al. 1815 (CR, UC).

PANAMA. COCLÉ: 7 km N of El Copé, area around Rivera Sawmill called Alto Calvario, 700-850 m, 21 Dec 1977, Folsom et al. 7071 (MO); El Copé, N del antiguo aserradero, 700-800 m, 22 May 1991, Valdespino et al. 1245 (NY, PMA);

3 hrs. de camino desde El Copé a Caño Susio, 700-800 m, 23 May 1991, Valdespino et al. 1249 (NY, PMA); Cordillera Central, 17.8 km desde la entrada de Llano Grande hacia Coclecito, 11 Jan 1992, Valdespino et al. 1363 (NY, PMA). PANAMÁ-SAN BLAS: along El Llano-Cartí road, ridge trail along the divide, 9°20'N, 78°58'W, 250-300 m, 12 Feb 1988, Moran 4106 (MO).

GUADELOUPE. 1856, Fée [probably collected by L'Herminier] (LG!).

COLOMBIA. NARIÑO: between Páramo and Barbacoas, 500 m, 7 May 1939, Alston 8468 (BM p.p.).

VENEZUELA. BOLÍVAR: La Gran Sabana, ca. km 202, S of El Dorado along road to Santa Elena, Salto Cama, ca. 1000 m, 4 Dec 1973, Davidse et al. 4878 (MO); near El Palmar, ca. 8°05'N, 61°50'W, ca. 75 m, 23 Nov 1967, Wessels-Boer 2064 (U). DELTA AMACURO: Antonio Díaz, 12 km S de San José de Amacuro, 8°28'N, 60°27'W, 0 m, Feb 1987, Fernández 3909 (NY).

TRINIDAD. ST. GEORGE: Aripo Savanna, 5 Mar 1920, N. Britton et al. 315 (NY), 1000 ft [300 m], 15 Jul 1963, Jermy 2302 (BM); Aripo, 27 Mar 1903?, Othner 138 (M). ST. ANDREW: Cumuto, near 5½ mile post, 13 May 1927, Broadway 7395 (BM, F); Quaré River Valley, ca. 600 ft [183], 25 Jan 1931, Totton (BM, P); Valencia road, 4-5 mile posts, 30 Mar 1930, Broadway 7730 (BM, K, MO, S-2 sheets, Z). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Hollis Reservoir road, 500 ft [152 m], 3 & 17 Jul 1984, Mickel 9474 (NY); Jururure river forest, 23 Feb 1930, Broadway 7694 (7694A at BM, K); Maraicaas, s.d., Jenman (NY); Morne Bleu ridge, from Textel station to Morne Bleu peak, 2400-2700 ft [732-823

m], 4 Jul 1984, Mickel 9489 (NY); Long Stretch, 25-26 mile post, 16 Mar 1928, Broadway 6813 (K-2 sheets), 6870 (K).

GUYANA. Arawau River, 16 Jul 1934, Archer 2338 (K, US); Baracara on the Mazaruni, Nov 1851, Barkly & Barkly (BM); vicinity of Bartica, on the Essequibo River, 3-12 Sep 1922, De la Cruz 1935 (F, GH, MO, NY, US); Bartica Grove, Nov 1886, Jenman 2322 (BM, K, US); opposite Bartica, Essequibo, Jenman 3640 (K, NY); between the Demerara and Berbice Rivers, 15-19 Jul 1922, De la Cruz 1608 (F, GH, MO, NY, US); Upper Demerara River, Jenman [4164] (BM, NY); ravines near the Kaieteur Fall, Jenman 1482 (K p.p., NY p.p.); Kara Kara creek, Jenman (NY); H.M.P.S. [near Kartabo, Essequibo], 14 Jun 1949, Guppy 1 [6093] (BM); Macouria creek, Essequibo River, Jenman (K, NY); region of Mt. Raywa, Jenman [2131] (NY p.p.); Makauria River [Macouria creek], Essequibo River, 22 Sep 1937, Sandwith 1568 (K); Mazaruni Station, 8 May 1933, Tutin 62 (BM); Upper Mazaruni River Basin, Utschi Falls, Kamarang River, 22 Oct 1960, S. Tillett & C. Tillett 45740 (NY, UC); Potaro region, Amatuk Falls, 31 Jul 1959, Whitton 38 (BM); Potaro River, between Tukeit and Kaieteur Savannah, 9 Sep 1937, Sandwith 1452 (K); Upper Rupununi River, near Dadanawa, 13 Jun 1922, De la Cruz 1529 (GH, NY, US).

FRENCH GUIANA. Cayenne, Leprieur (NY); l'Ile de Cayenne entre les embranchements de Tonnegrande et de Montsinery, 17 May 1979, Cremers 5667 (Z); Crique Charoein, 16 Feb 1914, Benoist 220 (P); Karouany, 1857, Sagot 749 (BM, GH, K, NY, S, W); Maroni, 1857, Sagot 1123 (K); Rivière Mana, Crique

Tamanoir, Hallé 586 (P, US); Oyapock, 1830, Leprieur (L); Rivuli Sourou amnis La Comte, 1847, Leprieur 167 (GH, P, US). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Herb. Ed. Jeanpert, s.c., F herb. No. 795041 (F); Leprieur (K, NY, P); 1834, Leprieur (UC); 1840, Leprieur (US); Leprieur 244 (A); Moricand (G).

ECUADOR: ESMERALDAS: Playa de Oro, 700 ft [213 m], Jul - Aug 1929, Thomas L.5 (K).

BRAZIL. MATO GROSSO: ca. 5 km N of Barra do Garças, 500 m, 7 May 1973, Anderson 9901 (AAU p.p., F, NY, UC). PARÁ: Serra do Cachimbo, 425 m, 12 Dec 1956, Pires et al. 6137 (NY).

WITHOUT SPECIFIC LOCALITY. In Antilles, (P).

NOMENCLATURAL COMMENTS: Alston et al. (1981) cited a collection "Upper Demerara River, Jenman s.n." as a syntype of S. platyphylla; this is incorrect since Baker (1885), in the original protologue, cited only a single collection, im Thurn, under this species.

The type of Lycopodium anomalum is apparently missing. J. P. Edwards (K) indicated in an annotation on the type cover of Lycopodium anomalum that the sheet containing the type collection, Ankers, was not found at K.

TAXONOMIC DISCUSSION: Alston et al. (1981) considered Selaginella porelloides as endemic to the Guianas. This species, however, has a continuous range in Continental America from Brazil to Costa Rica (Valdespino, 1993b), and

from the West Indies in Guadeloupe.

Selaginella porelloides is probably closely related to the Brazilian specimens of S. muscosa; differing in having idioblasts only on the lower surface (vs. on upper surface and obscure to conspicuous on the lower surface) of the lateral leaves, the median leaves with an acuminate (vs. long-acuminate to aristate) apex, white (vs. frequently yellow) megaspores, and ascending to erect (vs. mostly creeping) habit. Selaginella porelloides occasionally may be confused with S. seemannii, which see for discussion.

**8. *Selaginella seemannii* Baker, J. Bot. 21: 244. 1883.**

Type: NUEVA GRANADA [COLOMBIA]. CHOCÓ: Cacagual [Island], 1848, Seemann 1006 (Holotype: K!; isotype: fragment B!, BM!).

*Selaginella barbacoensis* Hieronymus, Hedwigia 43: 46. 1904.

Type: COLOMBIA. NARIÑO: Barbacoas, 6 Aug 1880, Lehmann 89 (Holotype: B-n.v.; isotype: BM!, G!).

Plants terrestrial or rarely epipetric. Stems ascending to erect, stramineous, 7-28 cm long, 0.5-1.5 mm diam., not articulate, not flagelliform, not stoloniferous, 2- or 3-branched. Rhizophores axillary, ventro-axillary to ventral, or occasionally with both a ventro-axillary and a dorsal rhizophore, restricted to basal  $\frac{1}{3}$  or less often to basal  $\frac{1}{2}$  of stem, 0.25-0.65 mm diam. Leaves dimorphic throughout, membranous, upper surface green, composed of rounded cells with sinuate walls, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant to slightly imbricate, perpendicular to the stem or slightly ascending, ovate-oblong to ovate-lanceolate, (2-)2.65-4  $\times$  1-2 mm; base subcordate to rounded, the acroscopic base strongly overlapping the stem, the basiscopic base not overlapping the stem; margins greenish to obscurely hyaline, acroscopic margin serrate throughout or only on basal  $\frac{1}{2}$  and on apical  $\frac{1}{4}$ , basiscopic margin mostly entire to serrulate along apical  $\frac{1}{3}$ ; apex broadly acute, dentate at tip; both surfaces glabrous, the upper surface without idioblasts, with obscure stomata along the basiscopic margin, the lower surface occasionally with

obscure idioblasts, with stomata along midrib. Median leaves distant, ascending, well spaced, broadly to narrowly ovate, or ovate-lanceolate,  $(1.25-1.6-2.85 \times (-0.7)1.-1.75$  mm; base asymmetric to oblique, the inner base truncate, the outer base with a well developed auricle; margins greenish to pale green, serrate to serrulate; apex acute to acuminate, the acumen  $\frac{1}{4}$  the length of the lamina, xx mm long, dentate at tip; both surfaces glabrous, without conspicuous idioblasts; the upper surface with stomata along midrib, the lower surface without stomata. Axillary leaves similar to lateral leaves, except frequently more cordiform and with the base cordate to rounded. Strobili terminal on branch tips, lax and flattened, dorsiventral, 0.4-2.0 cm long. Sporophylls partially dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along  $\frac{1}{4}$  to  $\frac{1}{2}$  the sporophyll length, asymmetric or ovate-lanceolate,  $2-2.5 \times 0.8-1$  mm, with a well developed and denticulate keel along midrib, the base rounded, the margins greenish, serrulate, the apex acute to shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without conspicuous idioblasts, with stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls; ventral sporophylls hyaline to slightly greenish, mostly ascending, pseudopeltately attached to the axis, ovate-lanceolate,  $1.5-2 \times 0.7-1.2$  mm, with an slightly developed and denticulate keel along midrib, the base rounded, the margins obscurely hyaline, serrulate, the apex short- to long-acuminate, the surfaces composed of elongate and hyaline cells

with sinuate walls, glabrous, without idioblasts, stomata present only along midrib of the lower surface. Megasporangia in two ventral rows or sometime occupying the entire strobilus; megaspores white, marguerite to massicot yellow (white to pale yellow), with a prominent equatorial flange, the proximal face striate to reticulate with open reticulum of low ridges, the distal face reticulate with open reticulum of high ridges, 250-320  $\mu$ m diam. Microsporangia in two dorsal rows or absent; microspores not studied.

HABITAT AND DISTRIBUTION: On soil in primary or disturbed forest, seasonally flooded forest, road banks, or wet rocks; 0-800 m; Panama, Colombia, Surinam, Ecuador, Peru, and Brazil.

SPECIMENS EXAMINED: PANAMA. COCLÉ: Bosque cercano a Coclecito, 28 Mar 1989, Galdames et al. 362 (PMA); Cerro Morenito cerca de Coclecito, 24.8 km desde la entrada de Llano Grande hacia Coclecito, 230 m, 10 Jan 1992, Valdespino et al. 1357 (BM, CR, K, MO, NY, PMA, UC, US).

COLOMBIA: NARIÑO: Barbacoas, 8 May 1939, Alston 8509 (BM, COL, US). VALLE DEL CAUCA: Buenaventura, Bridge over Dagua, near Buenaventura, 24 May 1939, Alston 8632 (AAU, BM, COL, NY, QCA, US); Carretera Cali-Buenaventura, Río Danubio inferior, ca. 200 m, 15 Sep 1967, Hagemann 425 (COL); Carretera Buenaventura-Cali, km 52, 300 m, Santa & Hoyos 757 (COL); Cordoba, orillas del Río Dagua, 100 m, 24 Feb 1984, Santa & Hoyos 751 (COL);



Sucre, near Buenaventura, 2 May 1878, Lehmann s.n. (W).

SURINAM. NICKERIE?: Upper Sipaliwini River., Camp 19, Morro Grande, 16 Feb 1936, Rombouts 489 (BM).

ECUADOR. ESMERALDAS: Road Lita-Alto Tambo, km 14, 0°47'N, 78°28'W, 800 m, 12 Jan 1991, Ollgaard 98787 (AAU); San Lorenzo, new road to "Proyecto NO," km 8-10, 19 Aug 1967, Sparre 18220 (S). NAPO: Estación Biológica Jatun Sacha, 1°4'S, 77°36'W, 450 m, 24 Aug 1988, Cerón & Cerón 4644 (MO, UC). NAPO-PASTAZA: Near Canelos, 300-400 m, 5 Nov 1935, Mexia 6906a (BM, UC, US). PASTAZA: Ceilán, Pica from Ceilán to Río Cononaco on the N side of Río Curaray, 1°36'S, 75°40'W, 200 m, 6 Jun 1980, Brandbyge & Asanza 31668 (AAU); Río Bobonaza, between oil exploration camp Chichirota and Destacamento Cabo Pozo, 2°25'S, 76°39'W, 20 Jul 1980, Ollgaard et al. 34850 (AAU). SANTIAGO-ZAMORA: Above Río Chupiantza, Valley of the Río Upano, from the Río Paute North ca. 17 km to the Chupiangas, 1950-2200 ft [594-671 m], 9 Dec 1944, Camp E-1444 (BM, NY); floodplain of Río Itzintza, Cordillera Cutucú, 2°40'S, 78°W, 3500-3700 ft [1067-1128 m], 17 Nov-5 Dec 1944, Camp E-1225 (NY); above Río Upano, near junction with Paute, near Mendez, 1750-2500 ft [533-762 m], 13 Nov 1944, Camp E-972 (BM, NY).

PERU. LORETO: Maynas, Yanamono, Explorama Tourist Camp, halfway between Indiana and mouth of Río Napo, 130 m, 3 Aug 1988, van der Werff et al. 9959 (MO, UC); Maynas, Explorama lodge, 2 Jul 1993, Montgomery 93-07 (NY, herb. J. Montgomery); Maynas, Río Itaya, ca. 10 km S of Iquitos, 13 Aug

1956, R. Tryon & A. Tryon 5195 (BM, U); along Río Itaya, May 1929, Llewelyn Williams 238 (BM); Soledad, on Río Itaya, ca. 110 m, 20 - 22 Sep 1929, Killip & Smith 29638 (NY, US).

BRAZIL. RORAIMA: Boa Vista, Reserva Ecológica de Maracá, track to Santa Rosa, ca. 600 m E of main Estação buildings, ca. 80 m, 12 Mar 1987, Edwards & Willikin 2541 (BM).

TAXONOMIC DISCUSSION: Selaginella seemannii is similar to and may be confused with S. porelloides. The former can be distinguished by ovate (vs. semicordate) lateral leaves with the upper surface glabrous throughout (vs. pubescent near the basiscopic margin), obtuse (vs. narrowly obtuse to slightly acute) apex, the lower surface with obscure (vs. with conspicuous) idioblasts, the base of the median leaves oblique with an outer auricle (vs. cordate to rounded, without auricles), and the base of the axillary leaves rounded (vs. usually cordate).

**9. *Selaginella gynostachya* Valdespino, sp. nov. (Map 2).**

Type: GUYANA. UPPER POTARO RIVER: vicinity of Kopinang village, 4°58'N, 59°50'W, 670 m, 29-Jul 1989, Boom & Samuels 8939 (Holotype: NY!; isotype: BRG-n.v.).

A *S. hyalogrammate* Valdespino et *S. karowtipuensi* Valdespino foliis intermediis basi subtruncatis vel rotundatis necnon foliis lateralibus supra idioblastis destitutis diversa; ulterius a prima foliis intermediis ellipticis, ovato-ellipticis vel ovatis, foliis lateralibus oblongis vel oblongo-ovatis necnon megasporis pallide luteis; ulterius a secunda foliis intermediis apice acutis vel breviter acuminatis.

Etymology--Gr., gyne, female or pertaining to female organs, and stachys, spike; referring to the mostly megasporangiate strobili found on specimens of this species.

Plants terrestrial. Stems creeping, stramineous, 5-14 cm long, 0.4-0.8 mm diam., not articulate, not flagelliform, not stoloniferous, 1- or 2-branched. Rhizophores axillary, restricted to basal ½ of the stem, stout, (0.28-) 0.34-0.56 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of ± rounded cells with slightly sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant,

slightly ascending, oblong to oblong-ovate,  $2.8-4 \times 1-1.9$  mm; base subtruncate to rounded, the acroscopic base strongly overlapping the stem, the basiscopic base not overlapping the stem; margins slightly hyaline, or pale green, the acroscopic margin serrate to ciliate-denticulate along basal  $\frac{1}{3}$ , serrulate apically, the basiscopic margin entire to serrulate apically; apex obtuse to broadly acute, dentate at tip; both surfaces glabrous, the upper surface without idioblasts, the lower surface frequently with conspicuous or obscure idioblasts, the stomata present only on lower surface. Median leaves distant, ascending, elliptic to ovate-elliptic,  $1.7-2.3 \times 0.7-1.4$  mm; base asymmetric with the inner base truncate and the outer base with an slightly developed auricle; margins slightly hyaline, serrate to serrulate; apex acute to shortly acuminate, the acumen, when present, less than  $\frac{1}{8}$  the length of the lamina,  $0.1-0.26$  mm long, puberulent and dentate at tip; both surfaces glabrous, the upper surface frequently with conspicuous idioblasts and stomata, the lower surface with obscure to conspicuous idioblasts, and without stomata. Axillary leaves similar to lateral leaves or more broadly ovate, except the base frequently rounded. Strobili terminal on branch tips and main stem apex, lax, flattened, and dorsiventral,  $5-15$  mm long. Sporophylls dimorphic, basally attached to the axis; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along ca.  $\frac{1}{2}$  to  $\frac{3}{4}$  the sporophyll length, asymmetric or lanceolate to lance-ovate,  $1.6-2.36 \times 0.6-0.98$  mm, with a strongly developed and slightly denticulate keel along midrib, the base  $\pm$  rounded, the margins slightly hyaline to hyaline-greenish, serrate to shortly ciliate, the apex acute to shortly

acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, frequently with conspicuous idioblasts and stomata, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls; ventral sporophylls almost colorless to pale green, ascending, with a slightly developed adaxial flap, ovate,  $1.48-1.9 \times 0.56-0.84$  mm, with a well developed and slightly denticulate to entire keel along midrib, the base attenuate to rounded, the margins hyaline to pale green, serrate to very shortly ciliate, the apex acute to shortly acuminate, both surfaces made of elongate and hyaline cells with sinuate walls, glabrous, with or without conspicuous idioblasts, the stomata present only along midrib on the lower surface. Megasporangia in two ventral rows; megaspores marguerite yellow (light yellow), with a well developed equatorial flange, the proximal face striate-reticulate to reticulate, the distal face reticulate with open reticulum of high ridges,  $300-320 \mu\text{m}$  diam. Microsporangia mostly absent from the two dorsal rows, or few mature near the apex on dorsal rows; microspores not studied.

**HABITAT AND DISTRIBUTION:** On stream or river banks; 900-1000 m; known from Venezuela, Guyana, and French Guiana.

**PARATYPES:** VENEZUELA. BOLÍVAR: Gran Sabana, ca. 10 km SW of Karaurin Tepui at junction of Río Karaurin Tepui and Río Asadon (Río Sanpa),

5°19'N, 61°03'W, 900-1000 m, Liesner 23798 (UC).

GUYANA. UPPER MAZARUNI: East bank of Waruma River, 20 km S of confluence with Kako River, 5°19'N, 60°46'W, 1000 m, Renz 14188 (U). Essequibo River of Porto Bartica, Jenman (K); Macouria River, Nov 1886, Jenman 2324 (BM, K, US); Macouria Creek, Essequibo River, Jenman (NY). UPPER POTARO RIVER: vicinity of Kopinang village, 4°58'N, 59°50'W, 670 m, 29 Jul 1989, Boom & Samuels 8939 (BRG-n.v., NY, type coll. of S. gynostachya).

FRENCH GUIANA. Rivière Sinnamary à Petit Saut, 12 Feb 1979, Cremers 5379 (Z).

TAXONOMIC DISCUSSION: Selaginella gynostachya seems more closely related to S. hyalogramma and S. karowtipuensis, but differs from them by the median leaves with a subtruncate to rounded (vs. rounded to semicordate as in S. hyalogramma or subcordate to rounded as in S. karowtipuensis) base and by lacking (vs. with) idioblasts on the upper surface of the lateral leaves. Selaginella gynostachya differs further from S. hyalogramma by elliptic to ovate-elliptic or broadly ovate (vs. lanceolate) median leaves, by oblong to oblong-ovate (vs. broadly ovate to broadly ovate-lanceolate) lateral leaves, and by marguerite yellow [light yellow] (vs. pinard- to baryta yellow [lemon yellow]) megaspores. Selaginella gynostachya differs from S. karowtipuensis also by its acute to shortly acuminate (vs. long-acuminate to short-aristate) apex.

**10. *Selaginella karowtipuensis* Valdespino, sp. nov. (Map 2).**

Type: GUYANA. UPPER MAZARUNI: Karowtipu Mountain, between camp and peak on western side of mountain, 5°45'N, 60°35'W, 920-1080 m, 24 Apr 1987, Boom & Gopaul 7698 (Holotype: NY!; isotypes: BM!, BRG!, PMA!, UC!, US!).

Selaginellae seemannii Baker affinis, sed foliis lateralibus, intermediis et sporophyllis superne idioblastis provisis diversa. A S. stenophylla A. Braun foliis intermediis basi non nisi auriculo exteriori integro vel serrulato provisis diversa.

Etymology--Named for the type locality.

Plants terrestrial. Stems creeping, stramineous, 20-34 (or more) cm long, 0.9-1.6 mm diam., not articulate, not flagelliform, not stoloniferous, 2- or 3(-4)-branched. Rhizophores axillary or occasionally with both axillary and dorsal rhizophores, restricted to basal ½ of the stem, stout, (0.44-)0.54-0.88 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of ± rounded cells with slightly sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant, perpendicular to the stem, oblong-ovate to oblong, 3-5.3 × 1.5-2.6 mm; base subcordate to rounded, the acroscopic base strongly overlapping the stem, the basisopic base not overlapping the stem; margins hyaline to pale green, the

acroscopic margin serrate, the basiscopic margin entire to serrulate apically; apex rounded to obtuse, dentate at tip; both surfaces glabrous, the upper surface with conspicuous idioblasts and without stomata, the lower surface with obscure idioblasts and with stomata along midrib. Median leaves distant, ascending, ovate to broadly ovate,  $2-3.1 \times 1-1.7$  mm; base subcordate, the inner base rounded and the outer base with a well developed auricle; margins hyaline, serrate; apex long-acuminate to short-aristate, the acumen or arista  $\frac{1}{4}$  or less the length of the lamina, 0.28-0.54 mm long, puberulent and dentate at tip; both surfaces glabrous, the upper surface with conspicuous idioblasts and the stomata along midrib, the lower surface with obscure idioblasts, without stomata. Axillary leaves similar to lateral leaves or more cordiform. Strobili terminal on branch tips and main stem apex, slightly lax and flattened, dorsiventral, 3-13 mm long. Sporophylls dimorphic, basally attached to the axis; dorsal sporophylls green, spreading, with an adaxial laminal flap extending along ca.  $\frac{1}{2}$  to  $\frac{1}{3}$  the sporophyll length, asymmetric or lanceolate to lance-ovate,  $1.54-2.08 \times 0.6-0.92$  mm, with a strongly developed and denticulate keel along midrib, the base rounded, the margins slightly hyaline to hyaline-greenish, serrate, the apex acute to shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with conspicuous idioblasts, the stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, and without idioblast; ventral sporophylls pale green, ascending to spreading, without an



adaxial flap, ovate,  $1.32\text{--}1.76 \times 0.6\text{--}0.9$  mm, with a well developed and slightly denticulate keel along midrib, the base rounded, the margins hyaline to pale green, serrate, the apex acute to shortly acuminate, the surfaces made of elongate cells with sinuate walls, glabrous, with idioblasts present only on lower surface, the stomata present only along midrib of the lower surface. Megasporangia in two ventral rows; megaspores maize yellow, with a prominent equatorial flange, the proximal face striate to reticulate with open reticulum of low ridges, the distal face reticulate with open reticulum of high ridges,  $320\text{--}340$   $\mu\text{m}$  diam. Microsporangia mostly absent from the two dorsal rows, or few mature near the apex on dorsal rows; microspores not studied.

HABITAT AND DISTRIBUTION: On sandy or rocky soil; 920-1080 m; known only from Karowtipu Mountain in Guyana.

PARATYPES: GUYANA. UPPER MAZARUNI: Karowtipu Mountain,  $5^{\circ}45'\text{N}$ ,  $60^{\circ}35'\text{W}$ , 920 m, 18 Apr 1987, Boom & Gopaul 7415 (BRG, MO, NY, P, PMA, U, UC, VEN), 920-1080 m, 24 Apr 1987, Boom & Gopaul 7698 (BM, BRG, NY, PMA, UC, US, type coll. of S. karowtipuensis).

TAXONOMIC DISCUSSION: Selaginella karowtipuensis resembles S. seemannii in its median leaves with a well developed outer auricle and acuminate apex, and, in general, oblong to oblong-ovate lateral leaves with subcordate to

rounded base. It can be easily distinguished from S. seemannii by having conspicuous (vs. without) idioblasts on the upper surface of the lateral and median leaves, and sporophylls. In addition, S. karowtipuensis is a more robust plant with stouter rhizophores.

**11. *Selaginella lychnuchus* Spring, Mém. Acad. Roy. Sci. Belgique 24: 247. 1849.**

Type: "COLOMBIA" [VENEZUELA]. MÉRIDA: Moritz 378 (Lectotype: B!, here designated; isoelectotype: LG!). Other syntype: "COLOMBIA" [VENEZUELA]. DIST. FEDERAL: Galipán, (same coll. as type of var. flaccida).

*Selaginella lychnuchus* Spring ex Klotzsch, Linnaea 20: 435. 1847, nom. nud.

*Selaginella lychnuchus* var. flaccida Spring, Mém. Acad. Roy. Sci. Belgique 24: 248. 1849.

Type: "COLOMBIA" [VENEZUELA]. DIST. FEDERAL: Galipán, Moritz 71 (Holotype: B-n.v.; isotypes: BM! [as 71?], G-2 sheets! [one as 71?, the other as 71 (p.p.)], K-2 sheets! [one as 71?, the other as 71], LG! [as 71?], P!).

*Selaginella lychnuchus* var. flaccida Spring ex Klotzsch, Linnaea 20: 436. 1847, nom. nud.

*Selaginella lychnuchus* var. rigidiuscula Spring, Mém. Acad. Roy. Sci. Belgique 24: 248. 1849, nom. superfl. for var. lychnuchus.

Type: "COLOMBIA" [VENEZUELA]. MÉRIDA: Moritz 378 (Holotype: B!; isotypes: LG!).

*Selaginella lychnuchus* var. rigidiuscula Spring ex Klotzsch, Linnaea 20: 436. 1847, nom. nud.

*Selaginella lychnuchus* var. pusilla A. Braun, Ann. Sci. Nat. Bot. V, 3: 288. 1865.

Type: VENEZUELA. DIST. FEDERAL: Caracas, Gollmer (Holotype: B-n.v.) [fide Alston et al., 1981: 276; Lellinger, 1989: 57.].

Plants terrestrial. Stems ascending to suberect, stramineous to greenish, 6-14 cm long, 0.4-1.1 mm diam., not articulate, not flagelliform, stoloniferous?, 1- or 2-branched. Rhizophores axillary, restricted to the basal  $\frac{1}{3}$  of the stem, filiform, 0.14-0.45(-0.6) mm diam. Leaves dimorphic throughout, thin-membranous, the upper surface green, composed of rounded cells with sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant, slightly ascending to perpendicular to the stem, ovate to ovate-lanceolate, or ovate-oblong,  $2.2-4.8 \times 0.8-2.3$  mm; base rounded, the acroscopic base slightly to strongly overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin slightly hyaline, long-ciliate near basal  $\frac{1}{2}$  and serrate to serrulate apically, or serrulate throughout, the basiscopic margin greenish, entire along basal  $\frac{1}{3}$  and serrulate along apical  $\frac{2}{3}$ , or entire throughout; apex broadly acute to obtuse, dentate at tip; the upper surface frequently with several long hairs, without idioblasts, the lower surface glabrous, with obscure idioblasts. Median leaves distant, ascending, broadly elliptic,  $1-2.4 \times 0.6-1.5$  mm; base asymmetric with the inner base truncate and the outer base decurrent, or oblique; margins hyaline (the inner margin more so), short-ciliate near the base to serrate apically, long-ciliate throughout, or serrulate throughout; apex long-aristate, the arista to more than half of lamina length, 0.6-1.5 mm long, greenish, puberulent; the upper surface glabrous, with obscure to conspicuous idioblasts, with stomata along midrib and at the outer base, the lower surface glabrous, without idioblasts and stomata. Axillary leaves similar to lateral leaves or slightly more ovate-lanceolate. Strobili

terminal on branch tips, lax, flattened, and dorsiventral, 3-14 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along ca.  $\frac{1}{2}$  to  $\frac{2}{3}$  the sporophyll length, asymmetric or lanceolate to ovate-lanceolate,  $1.2-2.8 \times 0.3-0.8$  mm, with a strongly developed denticulate keel along midrib, the base rounded, the margins hyaline, short-ciliate basally to serrulate apically, the apex acuminate, the upper surface green composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with obscure to conspicuous idioblasts and stomata throughout, the lower surface silvery, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls almost colorless to completely hyaline, ascending, pseudopeltately attached to the axis, without an adaxial flap, ovate-lanceolate,  $1.2-1.6(-2.1) \times 0.4-0.6$  mm, with a slightly developed denticulate keel along midrib, the base rounded, the margins hyaline, short-ciliate, the apex long-acuminate to short-aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, with conspicuous to obscure idioblasts, without conspicuous stomata. Megasporangia in two ventral rows; megaspores maize yellow, cream, pale yellow-orange, or pale orange-yellow, without an equatorial flange, the proximal face striate-reticulate with close to open reticulum of moderately high ridges, the distal face reticulate with open reticulum of rather high ridges,  $240-290 \mu\text{m}$  diam. Microsporangia in two dorsal rows or absent, if absent then dorsal sporophylls sterile; microspores not studied.

**HABITAT AND DISTRIBUTION:** On shaded and moist premontane to montane forest or steep river banks; 800-2220 m; Guatemala, Costa Rica, Colombia, and Venezuela.

**SPECIMENS EXAMINED: GUATEMALA. ALTA VERAPAZ:** Pansamalá, 3800 ft [1159 m], Apr 1889, J. D. Smith 1578 (K, US); Pansamalá, 3800 ft [1159 m], Jan 1886, von Türckheim 832 (GH, NY).

**COSTA RICA. CARTAGO:** Tapantí, Río Grande de Orosi, 1200 m, 19 Jan 1964, Jiménez 1597 (CR, F); Tapantí, ca. 15 km S of Paraíso, 1150 m, 20 Mar 1967, Mickel 1922 (NY), 3 Jul 1967, Mickel 2310 (NY p.p.). **SAN JOSÉ:** 1 km N of La Hondura on Rte 220 between Volcán Irazú and Volcán Barva, 1500 m, 9 Jul 1967, Mickel 2568 (NY); La Hondura, 1300-1700 m, 2-4 Mar 1924, Standley 36193, 36279 (BM, US).

**COLOMBIA. SANTANDER:** Bucaramanga, Corba [Corcocova] near Bucaramanga, 2200 m, 27 Feb 1939, Alston 7311 (US); Bucaramanga, La Corcova, 2220 m, 22 Sep 1983, Santa & Buitrago 918 (COL, HUA).

**VENEZUELA. ARAGUA:** La Regresiva, Parque Nacional, km 25, 1000 m, 2 Dec 1938, Ll. Williams & Alston 170 (AAU p.p., BM, US), 10773 (F). **FALCÓN:** Sierra de San Luis, entre Sta. Lucía y Cabure, 800 m, 28 Jun 1979, Flora Falcón (HW,BV) [Wingfield] 869 (U, UC). **DIST. FEDERAL:** Galipán, Moritz 71 (B-n.v., BM!, G!-2 sheets (one p.p.), K!, LG!, P!, type coll. of Selaginella lychnuchus var. flaccida), Moritz 71 & 221 (US p.p.), Moritz 221 & 71 (BM). **MÉRIDA:** Moritz 378

(B-n.v., LG!, type coll. of Selaginella lychnuchus var. rigidiuscula), Moritz 378 & 71? (BM); Río Albariga, N of Mérida, 2400 m, 9 Feb 1939, Alston 6969 (BM); Sucre, N de La Trampa, 9°34'N, 71°26'W, 2000 m, 2 Feb 1987, Ortega et al. 3042 (UC). SUCRE: Cumaná, Quebrada del Imposible, Moritz 221 & 71 (BM).

NOMENCLATURAL COMMENTS: When Spring (1849) described this species he cited only two specimens that he had seen at Hb. Berol. (B): Mérida, Moritz 378 and Galipán, Moritz 71, representing, respectively, his var. rigidiuscula and var. flaccida. Badré (1983) erroneously considered duplicates of both collections at LG as holotypes of the two varieties. I consider, in accordance with the International Code of Botanical Nomenclature [ICBN] (Greuter, 1994), that the implicit holotypes of these two varieties are the two specimens at B originally cited by Spring (1849), and that the duplicates at LG are isotypes.

There is much confusion regarding Moritz's collection numbers. Alston et al. (1981: 272, but see also p. 277.), in a note commented, "It appears that the determiner [A. Braun ?] of Moritz collections sorted them into species groups when gatherings were mixed. We therefore find labels bearing "71 & 221," meaning that the material thus distributed with that label came from both field collections". It is not certain, however, whether this explanation is correct. In this study, I have found several specimens labelled, e.g., Moritz 71, Moritz 71?, Moritz 71 & 221, Moritz 221 & 71, Moritz 378 & 71?, and Moritz 71? & 378. Some of them are S. lychnuchus, as currently interpreted (see specimens cited under S.

lychnuchus var. flaccida and var. rigidiuscula, and Moritz 221 & 71 at BM); others are mixed collections containing S. lychnuchus, S. tenella (P. Beauv.) Spring (syn.: S. cladorrhizans A. Braun), and S. flacca Alston (e.g. Moritz 71 & 221 at US), or S. lychnuchus and S. pallescens (C. Presl) Spring (e.g., Moritz 71 at G), some are S. tenella (e.g., Moritz 71<sup>?</sup> at O, S, and Moritz 71 & 221 at BM), S. flacca (see specimens cited under it), or S. flagellata Spring (i.e., Moritz 71<sup>?</sup> & 378). Unfortunately, I did not receive the holotype of S. lychnuchus var. flaccida among the types sent on loan to me by B, and therefore cannot be completely sure as to whether or not Moritz 71 at B is indeed S. lychnuchus, or S. flacca, or even S. tenella. Taking into account these problems, I have decided to choose as the lectotype of S. lychnuchus the syntype Moritz 378 (Lectotype: B; islectotype: LG), because there is less confusion associated with the identity of this collection, and to provisionally include var. flaccida as a synonym of it. I have also decided to exclude as type material of S. lychnuchus and of its two original varieties specimens that bear two collection numbers and were not originally cited by Spring, more specifically, Moritz 378 & 71<sup>?</sup> (BM). This specimen was cited by Alston et al. (1981) as Moritz 378 (BM), although it bears the two collection numbers previously referred to. I also have excluded, as type material of var. flaccida, Moritz 71 & 221 at US and Moritz 221 & 71 at BM. All three of them probably contain specimens from different collections, and it is not possible to assess to which collection number they correspond.



TAXONOMIC DISCUSSION: Selaginella lychnuchus may be confused with S. flagellata because of their strongly dimorphic sporophylls, seemingly absent microsporangia, and ascending to erect habit (sometimes also found in S. flagellata). They differ from the latter by their light yellow, cream, or occasionally orange megaspores, and the asymmetric base of the median leaves.

The long hairs on the upper surface of the lateral leaves are hyaline, and thus are often difficult to observe due to the light incidence angle on a dissecting microscope. They are easy to observe under a compound microscope or by changing the light incidence angle on a dissecting microscope.

The collections examined from Guatemala had megaspores with a deeper orange color (i.e., orange-buff to capucine yellow). Both collections were previously referred to by Alston (1955) as S. porphyrospora, and represent the northernmost extension of the species range.

Specimens from South America, particularly from Colombia, had longer cilia on the margins of the lateral and median leaves, and possessed more conspicuous idioblasts on the upper surface of the median leaves than collections from Central America. Unfortunately, I have seen few specimens from Central America. This makes it risky to speculate whether or not differences between populations from Central and South America are constant, whether they indeed correlate with any geographic pattern, or whether they represent the normal variation within the species. Therefore, I prefer to recognize a single taxon, which varies in the characteristics mentioned above.

A specimen, Ll. Williams & Alston 144 (BM!), cited by Alston et al. (1981),  
under S. lychnuchus is actually S. popayanensis Hieron.

**12. *Selaginella ramosissima* Baker, J. Bot. 23: 295. 1885.**

Type: PERU. LORETO: near Tarapoto, 1855-6, Spruce 4088 (Holotype: K!; isotypes: B!, BM-2 sheets!, BR!, CGE-n.v., LG!, NY-2 sheets! [one a fragment], OXF!, P!, W!).

Plants terrestrial. Stems ascending to suberect, stramineous to greenish, 6-18 cm long, 0.6-1.6 mm diam., not articulate, not flagelliform, occasionally stoloniferous, 2- or 3-branched. Rhizophores axillary, restricted to the basal  $\frac{1}{3}$  of the stem, filiform, 0.2-0.56(-0.6) mm diam. Leaves dimorphic throughout, thin-membranous, the upper surface green, composed of rounded cells with sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant, slightly ascending to perpendicular to the stem, ovate-oblong to oblong,  $1.8-3 \times 0.6-1.4$  mm; base rounded, the acroscopic base slightly overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin slightly hyaline to greenish, serrulate to entire, the basiscopic margin greenish, entire to serrulate (especially along apical  $\frac{1}{3}$ ); apex broadly acute to obtuse, dentate at tip; the upper surface glabrous, without idioblasts, the lower surface glabrous, with conspicuous or obscure idioblasts. Median leaves distant, ascending, narrowly elliptic,  $1.4-2 \times 0.5-0.8$  mm; base asymmetric with the inner base truncate and the outer base decurrent, or oblique; margins narrowly hyaline, serrulate to entire; apex gradually long-aristate, the arista  $\frac{1}{3}$  to  $\frac{1}{2}$  of lamina length, 0.3-0.5 mm long, greenish, puberulent; both surfaces glabrous, without conspicuous

idioblasts. Axillary leaves similar to lateral leaves or slightly more ovate-lanceolate. Strobili terminal on branch tips, lax, flattened, and dorsiventral, 3-13 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along ca.  $\frac{1}{2}$  to  $\frac{2}{3}$  the sporophyll length, asymmetric, oblong to oblong-lanceolate, or oblong-ovate,  $1.3-1.9 \times 0.3-0.6$  mm, with a strongly developed denticulate to entire keel along midrib, the base rounded, the margins hyaline, serrate to serrulate, the apex acuminate to broadly acute, the upper surface composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts, with conspicuous stomata, the lower surface silvery, composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts or stomata; ventral sporophylls almost colorless to completely hyaline, ascending, pseudopeltately attached to the axis, without an adaxial flap, ovate-lanceolate,  $1-1.5 \times 0.4-0.55$  mm, with a slightly developed denticulate to entire keel along midrib, the base rounded, the margins hyaline, serrate, the apex long-acuminate to aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, with conspicuous to obscure idioblasts, without conspicuous stomata. Megasporangia in two ventral rows; megaspores cream to marguerite yellow (light-yellow), with an equatorial flange, the proximal face rugulate-reticulate to striate-reticulate with open to close reticulum of rather low ridges, the distal face reticulate with open reticulum of high ridges,  $220-235 \mu\text{m}$  diam. Microsporangia in two dorsal rows or absent, if absent then dorsal sporophylls sterile; microspores

tan to orange, without an equatorial flange, the proximal face seemingly smooth, the distal face verrucate to seemingly smooth, 19-32  $\mu\text{m}$  diam.

**HABITAT AND DISTRIBUTION:** On river banks in moist premontane to montane forest; 450-2133 m; Ecuador and Peru.

**SPECIMENS EXAMINED:** ECUADOR. NAPO: Reserva Biológica Jatun Sacha, 8 km de Puerto Misahuallí, margen derecho del Río Napo, 1°04'S, 77°36'N, 450 m, 4 Sep 1987, Cerón et al. 2175 (MO). SANTIAGO-ZAMORA: Valley of the Río Zamora, E of Loja, along trail between Río Sabanilla and Canillones Tambo, 1371-2133 m, 28 Jun-1 Jul 1944, Camp E-66 (US), Camp E-66a (NY). ZAMORA-CIINCHIPE: Quebrada de Palanuma, 1015 m, 8 Jul 1989, Valdespino & Dorr 1077 (NY, PMA, QCA); N of Zamora, 4°04'S, 78°57'W, 1000-1200 m, 13 Jun 1988, Øllgaard et al. 74811 (AAU, QCA); 8.6 km W of Zamora on Zamora-Loja road, 4°01'S, 79°01'W, 1200-1300 m, 14 Jul 1989, Valdespino & Dorr 1109 (NY); 8.5 km W of Zumbi, 3°55'S, 78°53'W, 955 m, 12 Jul 1989, Valdespino & Dorr 1100 (NY, PMA, QCA); 3-8 km E of Paquisha. 3°55'S, 78°35'W, 1077 m, 13 Jul 1989, Valdespino & Dorr 1103 (NY, PMA, QCA).

PERU. CAJAMARCA: Monte Seco, Hualgayoc, 1800 m, Soukup 3872 (BM-n.v., fide Alston et al., 1981: 277.). LORETO: near Tarapoto, 1855-6, Spruce 4088 (B, BM-2 sheets, BR, CGE-n.v., K, LG, NY, OXF, P, W, type coll. of S. ramosissima); near Tarapoto, 1855-6, Spruce 4088a (B).

TAXONOMIC DISCUSSION: Selaginella ramosissima can be confused with Selaginella lychnuchus, but differs from it by having the acroscopic margin of the lateral leaves serrate (vs. usually ciliate) along the basal  $\frac{1}{2}$ , with the upper surface glabrous (vs. usually with long hairs), the median leaves with the arista up to (vs. more than) half of the lamina length, and without (vs. usually with) conspicuous idioblasts.

Valdespino & Dorr 1109 (NY) differs from other specimens in having the acroscopic margin of the lateral leaves and both margins of the median leaves more broadly hyaline, the lateral leaves with the acroscopic margin definitively serrate, and the presence of stolons at the base of the stem. In these characteristics, this specimen is more similar to S. chionoloma, but the orangish color of its megaspores is more similar to typical S. ramosissima. I prefer to treat Valdespino & Dorr 1109 within S. ramosissima until additional biosystematic studies can be carried out on S. ramosissima and S. chionoloma (see additional comments under S. chionoloma).

13. *Selaginella chionoloma* Alston ex Crabbe & Jermy, Amer. Fern J. 63: 137.

1973.

Type: PERU. [Cuzco:] Cuquipata, Valle de Lares, Feb 1928, F. Herrera  
1636 (Holotype: US!; isotype: BM!).

Plants terrestrial. Stems suberect to erect, stramineous or greenish, 7-20 cm long, 0.34-0.8 mm diam., not articulate, occasionally flagelliform, stoloniferous, 2- or 3-branched. Rhizophores axillary, restricted to basal  $\frac{1}{4}$  or occasionally to basal  $\frac{1}{2}$  of the stem, filiform, 0.08-0.16 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, ovate-oblong or oblong,  $1.8-2.8 \times 0.8-1.5$  mm; base rounded to semicordate, the acroscopic base strongly overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin broadly hyaline, especially along basal  $\frac{1}{2}$ , serrate along basal  $\frac{2}{3}$ , serrulate apically, the basiscopic margin narrowly hyaline or pale green, entire to sparsely serrulate, the basiscopic margin without conspicuous stomata; apex acute, dentate at tip; the upper surface glabrous, without idioblasts or stomata, the lower surface glabrous, usually with conspicuous idioblasts, and with stomata along midrib. Median leaves distant, ascending, narrowly elliptic or narrowly elliptic-ovate,  $1.1-1.5 \times 0.48-0.7$  mm; base oblique or asymmetric, if asymmetric then with the inner base  $\pm$  truncate and the outer base

decurrent; margins hyaline, sparsely serrate; apex gradually long-aristate, the arista about or occasionally more than  $\frac{1}{2}$  the length of the lamina, 0.5-0.7 mm long, frequently puberulent, dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib, the lower surface without idioblasts or stomata. Axillary leaves similar to lateral leaves, except the base rounded, and both margins usually serrate to serrulate throughout. Strobili terminal on stem and branch apices, lax and flattened, dorsiventral, 2-10 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{1}{2}$  to  $\frac{3}{4}$  the sporophyll length, asymmetric, lanceolate, or lance-ovate,  $1.1-1.48 \times 0.38-0.54$  mm, with a strongly developed, denticulate keel along midrib, the base rounded, the margins broadly hyaline, serrate becoming serrulate apically, the apex acute to shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts, with stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis, without an adaxial flap, ovate,  $1.22-1.4 \times 0.46-0.64$  mm, with a well developed, denticulate keel along midrib, the base rounded, the margins broadly hyaline, serrate becoming serrulate apically, the apex long-acuminate to shortly aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present only



on the lower surface. Megasporangia generally in two ventral rows or occupying the basal ½ of the ventral rows; megaspores orange-buff, without an equatorial flange, the proximal face rugulate or seemingly smooth, the distal face reticulate with open reticulum of moderately high ridges, 220-240 µm diam. Microsporangia in two dorsal rows, frequently also on the apical region of ventral side of strobili, or strobili wholly microsporangiate; microspores tan to orange, without an equatorial flange, the proximal face seemingly smooth, the distal face verrucate to seemingly smooth, 26-32 µm diam.

**HABITAT AND DISTRIBUTION:** On shaded banks; 800-1610 m; Peru and Bolivia.

**SPECIMENS EXAMINED:** PERU. CUZCO: Convención, Hda. Potrero, 1300 m, 3 Mar 1942, Vargas 2491 (UC); Cuquipata, Valle de Lares, Feb 1928, E. Herrera 1636 (BM, US-n.v., type coll. of S. chionoloma). SAN MARTÍN: Tingo María, beyond Las Palmas, 800 m, 30 Oct 1949 - 19 Feb 1950, Allard 21130 (BM).

**WITHOUT SPECIFIC LOCALITY:** Matthews 1084 (OXF) [1084 at other herbaria, e.g., NY! is S. novae-hollandiae, see Alston et al., 1981: 275.].

**BOLIVIA. LA PAZ:** Nor Yungas, road between Unduvai and Pte. Villa, 1610 m, 11 Mar 1980, Hickey & Eshbaugh 768 (AAU, GH); Sur Yungas, La Florida, ca. 1900 m, 8 Dec 1920, Asplund 1602 (S).

TAXONOMIC DISCUSSION: I hesitate to recognize S. chionoloma at the species level because it is very closely related to and may be easily confused with S. ramosissima. Already Crabbe & Jermy (1973) expressed some doubts as to whether or not this taxon should be treated as new. They correctly pointed out that it was most distinct by having the leaves with broadly hyaline ("white") margins. Alston et al. (1981) compared S. chionoloma with S. ramosissima and distinguished them by the former having thin (vs. stouter) stems, which lack (vs. have) stolons, and the acroscopic margins of the lateral leaves broadly hyaline (vs. slightly hyaline to greenish). I agree partially with this characterization; however, the stems on the type collection of S. chionoloma are quite stout, not thin as defined by Alston et al. (1981). In general, I have found that in S. chionoloma the margins of the median leaves and the acroscopic margin of the lateral leaves tend to be distinctly serrate, whereas in S. ramosissima they tend to be serrulate to entire. Another feature that may help to distinguish these two species are the orange-buff megaspores found in three of the specimens here cited under S. chionoloma (Hickey & Eshbaugh 768, Matthews 1084, and Vargas 2491), whereas megaspores in S. ramosissima are usually cream to marguerite yellow. Unfortunately, no megaspores have been observed from the type collection of S. chionoloma, and therefore I could not confirm that this characteristic is definitively a trait of this species. On the other hand, most of the other morphological characteristics of specimens representing both species are almost entirely alike. In addition, as previously discussed under S. ramosissima, there is

a collection from Ecuador, Valdespino & Dorr 1109, that has some characteristics resembling both S. chionoloma and S. ramosissima, and that I provisionally referred to the latter. This collection suggests that these two taxa are very closely related and may be part of the same taxon, which may be best treated as varieties of a single species rather than as two distinct taxa.

Selaginella chionoloma has been recently synonymized under S. novae-hollandiae by R. Tryon and Stolze (1994), but it is considered here as a distinct species not closely related to the latter. Selaginella chionoloma differs chiefly from S. novae-hollandiae by having the base of the median leaves not auricled (vs. with a conspicuous and free from the stem, outer auricle, and frequently -at least in Peruvian material- with a less developed inner auricle) and the base glabrous (vs. auricles frequently tufted with short hairs), the acroscopic margin of the lateral leaves serrate to serrulate (vs. long-ciliate at least along the basal  $\frac{1}{2}$  to  $\frac{3}{4}$ ), the axillary leaves serrate to serrulate (vs. long-ciliate at least along basal  $\frac{1}{2}$  to  $\frac{3}{4}$ ), and orange-buff (vs. snow- to bone-white or light cream) megaspores. Some of the Peruvian specimens of S. novae-hollandiae, which were presumably, equated with S. chionoloma by R. Tryon and Stolze (1994), may eventually prove to be a new species, possibly, in subg. Heterostachys (see Appendix II).

**14. *Selaginella popayanensis* Hieronymus, Hedwigia 43: 9. 1904. (Figs. 1B & D; 13A-G).**

Type: COLOMBIA. CAUCA: near Popayán, 1600-2000 m, Feb, Lehmann 6968 (Holotype: B!; isotype: K-n.v., US!).

*Selaginella anisoclada* Alston ex Crabbe & Jermy, Fern Gaz. 11: 255. 1976, syn. nov.

Type: VENEZUELA. ARAGUA: above Guamitas, Parque Nacional, 900 m, 30 Dec 1938, Alston 5814 (Holotype: BM!; isotype: US!).

*Selaginella disticha* Mickel & Beitel, Mem. New York Bot. Gard. 46: 337. 1988, syn. nov.

Type: MEXICO. OAXACA: Dist. Ixtlán, 7 km S of Vista Hermosa, 5400' [1645 m], 23 Sep 1972, Mickel 6735 (Holotype: NY!; isotype: UC!).

Plants terrestrial or epipetric. Stems creeping or ascending to suberect, stramineous to greenish, 4-12 cm long, 0.3-0.6 mm diam., not articulate, not or infrequently flagelliform, stoloniferous or not, 2- or 3-branched. Rhizophores axillary, throughout or restricted to basal ½ of the stem, filiform, 0.12-0.22 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of ± rounded cells with sinuate walls, the lower surface silvery green, composed of elongate cells with sinuate walls. Lateral leaves distant, perpendicular to the stem or ascending, ovate to ovate-oblong, 1.5-3.1 × 1.0-1.8 mm, base rounded, the acroscopic base strongly overlapping the stem, the

basispic base not overlapping the stem, margins greenish to pale green, sparsely serrulate to entire; apex acute, denticulate at tip; the upper surface hispid near the basispic margin, without idioblasts or stomata, the lower surface glabrous, with obscure idioblasts, and with stomata along midrib. Median leaves distant, ascending, ovate-lanceolate,  $0.84-1.5 \times 0.4-0.94$  mm; base asymmetric to rounded; margins hyaline, serrate to serrulate; apex acute, gradually short- to long-acuminate, the acumen  $\frac{1}{4}$  or less the length of the lamina,  $0.1-0.24$  mm long, dentate at tip, both surfaces glabrous, without idioblasts, the upper surface with stomata along midrib, the lower surface without stomata. Axillary leaves similar to lateral leaves, except the margins minutely serrulate on basal  $\frac{1}{4}$ , entire apically. Strobili terminal on branch tips and main stem apex, lax and flattened, dorsiventral, (2-)4-15 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along ca.  $\frac{1}{2}$  to  $\frac{3}{4}$ , or throughout the sporophyll length, asymmetric or lanceolate to lance-ovate,  $(1.48-1.54-2.36 \times 0.7-0.9)$  mm, with a strongly developed and denticulate keel along midrib, the base rounded, the margins hyaline, serrate to serrulate, the apex short to long-acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous or occasionally hirsute, without idioblasts, and with stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis,

without an adaxial flap, ovate to ovate-lanceolate,  $1.3-1.8 \times 0.54-0.94$  mm, with a slightly developed denticulate to entire keel along midrib, the base rounded, the margins hyaline, serrulate, the apex acute or short- to long-acuminate, both surfaces composed of elongate cells with sinuate walls, glabrous, with obscure idioblasts, the stomata present only on the lower surface. Megasporangia in two ventral rows; megaspores orange-buff, light orange-yellow, or deep chrome (light orange to orange), frequently with a prominent equatorial flange, the proximal face reticulate, reticulate-striate, or corrugate-reticulate with open to close reticulum of moderately high ridges or corrugate-reticulate, the distal face reticulate or reticulate-corrugate with open reticulum of low and coarse or high ridges,  $240-295 \mu\text{m}$  diam. Microsporangia in two dorsal rows or absent from it; microspores not studied.

**HABITAT AND DISTRIBUTION:** On ground or wet mossy rocky banks in wet montane forest; 1100-2700 m; Mexico, Guatemala, Costa Rica, Panama, Colombia, Venezuela, and Bolivia.

**SPECIMENS EXAMINED:** MEXICO. CHIAPAS: Puerto Viendo near Rincón Chamula, 6000 ft [1830 m], 20 Aug 1967, Gittins 4238-B (NY); Rayón, Selva Negra, 10 km above Rayón Mezcalapa along road to Jitotol, 1700 m, 25 Jan 1973, Breedlove & A. R. Smith 32239 (MICH-2 sheets), 32339 (DS, F), 27 Jan 1973, Breedlove & A. R. Smith 32680 (DS, NY). GUERRERO: Atoyac de Alvarez, ca. 2

km SE de El Molote, 1620 m, 16 Apr 1984, Lorea 2998 (F, NY). OAXACA: 47 mi from Ixtlán on Mex. 175, 19 Jun 1972, McAlpin 1022 (CAS p.p., F); Ixtlán-Tuxtepéc road, 35-39 km S of Valle Nacional (km 96-100), 4500-5200 ft [1372-1586 m], 27 Jul 1964, Mickel 1560 (NY); Ixtlán, 65-68 km N of Ixtlán, 41-44 km S of Valle Nacional, 6200 ft [1891 m], 28 Oct 1969, Mickel 4295 (NY); Villa Alta, 5-10 mi NE of Villa Alta on trail to Yelagago Valley, 5000 ft [1525 m], 4 Aug 1962, Mickel 1110 (MICH).

GUATEMALA. ALTA VERAPAZ: Chihob, 3000 ft [915 m], 23 Oct 1920, Johnson 823 (US); road between Tactic and the divide on road to Tamahú, 1500-1600 m, 1-7 April 1941, Standley 90582 (F); Pansamalá, 3800 ft [1159 m], Jan 1886, von Türckheim 832 (K, US-2 sheets). QUEZALTENANGO: Finca Helvetia, near Retalhues, 5000 ft [1525 m], 2 May 1937, Muenschner 12165 (US), 12166 (US), 12167 (US); above Mujuliá, between San Martín Chile Verde and Colomba, ca. 1800 m, 1 Feb 1941, Standley 85466, 85548 (US); western slopes of Volcán Zunil, opposite Santa María de Jesús, 1500 m, 21 Jan 1940, Steyermark 35154 (F).

COSTA RICA. ALAJUELA: La Palma de San Ramón, 1250 m, 14 Jan 1930, Brenes 12010<sup>a</sup> (367<sup>a</sup>) (CR). CARTAGO: Tapantí, ca. 15 km S of Paraíso, 1150 m, 20 Mar 1967, Mickel 1925 (NY); Refugio Nacional de Fauna Silvestre Tapantí, sendero Oropéndula y riberas adyacentes del Río Grande de Orosi, 27 Nov 1991, Valdespino 1264 (CR, NY, PMA); ca. 16 km S de Paraíso, "Quebrada Seca" ca. 300 m antes del puente sobre el Río Grande de Orosi, 10 Dec 1991, Valdespino 1285 (CR, NY, PMA, UC, US). HEREDIA: Cinchona, above the Upper Sarapiquí

Valley, 4000 ft [1220 m], 20 Mar 1955, Scamman 7542 (US p.p.); Yerba Buena, NE of San Isidro, ca. 2000 m, 22, 28 Feb 1926, Standley & Valerio 49176 (BM, F, US). **PUNTARENAS:** Monteverde Cloud Forest Reserve, 1450-1580 m, 17 Jun 1980, Lee 81 (UC). **SAN JOSÉ:** Vicinity of La Hondura, 4 km S to 1 km N on Rte 220, between Volcán Irazú and Volcán Barva, 1250-1500 m, 25 Mar 1967, Mickel 2251 (NY); between La Palma and La Hondura, 1-4 km S of La Hondura on Rte 220, between Volcán Irazú and Volcán Barva, 1500 m, 9 Jul 1967, Mickel 2518 (NY); ca. 10 km of San Rafael de Heredia on Volcán Barva, 1950 m, 13 Jul 1967, Mickel 2646 (NY); La Palma, 1400 m, 17 Mar 1908, Brade & Brade 222 [also labeled only as Brade 222] (BM, US), 26 Mar 1908, Brade 72 (UC), 22 Jun 1910, Brade & Brade 222 [also labeled only as Brade 222] (NY, UC, US), 1600 m, 17 Mar 1924, Standley 38063 (US).

**PANAMA. CHIRIQUÍ:** Upper Caldera watershed, between "Camp 1" and the Divide, Holcomb's trail, above El Boquete, 1650-1925 m, 23 Mar 1911, Maxon 5642 (BM, US); Bugaba, Fortuna, quebrada al lado del vivero del IRHE, 12 Jan 1989, Valdespino et al. 917 (PMA, NY), 3 May 1991, Valdespino & Ríos-Levi 1209 (PMA); Presa de Fortuna, desviación a la izquierda (NW) después de pasar el puente sobre el embalse, 17.15 km N de los Planes de Hornito, 3 May 1991, Valdespino & Ríos-Levi 1208 (PMA), 3 Jan 1992, Valdespino et al. 1336 (NY, PMA). **CHIRIQUÍ-BOCAS DEL TORO:** Trocha de Palo Seco, 2 May 1991, Valdespino & Ríos-Levi 1184 (fragment NY, PMA).

**COLOMBIA. MAGDALENA:** Sierra del Libano, Santa Marta, 5500 ft [1677



m], Mar 1898-89, H. H. Smith 2242 (GH, BM, F, K, MICH, MO, NY-2 sheets, P, S-2 sheets, U, US); Sierra Nevada de Santa Marta, Alto Río Buritaca, Ciudad Perdida, Buritaca 200, 11°04'N, 73°48'W, 1100 m, 18 Jul 1989, Madriñán & Barbosa 391 (MO); Sierra Nevada de Santa Marta, carretera a La Cuchilla, 1650 m, 9 May 1983, Santa & Escobar 633 (COL); Santa Marta, Cincinati, 1900 m, 17 Jan 1967, Mägdefrau 1136 (COL, M); Santa Marta, 1898-1901, H. H. Smith 2567 (BM p.p.). VALLE DE CAUCA: near Queremal, 1300 m, 5 Apr 1939, Alston 7906 (AAU, BM, COL, NY, QCA, US).

VENEZUELA. ARAGUA: Colonia Tovar, 5000 ft [1525 m], 1854-1855, Fendler 402 (K, YU); abajo de Rancho Grande, Parque Nacional, 1900 m, 12 Jan 1938, Ll. Williams & Alston 10747 (F); below Rancho Grande, Parque Nacional, 1000 m, 1 Dec 1938, Ll. Williams & Alston 144 (BM, F).

BOLIVIA. LA PAZ: Murillo, Valle de Zongo, 32 km N of (below) La Cumbre, ca. 4.4 km above Zongo, trail up Río Jachcha Cruz valley, ca. 16°04'S, 68°04'W, 2200-2300 m, 11 May 1990, Luteyn & Dorr 13654 (NY, PMA, UC); Nor Yungas, 6 km NE of Chuspipata on the road to Coroico, 16°17'S, 67°48'W, 2700 m, 21 Feb 1986, Solomon 14972 (AAU, F, MO, UC); Yungas, Jul 1893, Jay c (NY), Jay e (NY), 6000 ft [1830 m], 1885, Rusby 462A (NY). WITHOUT SPECIFIC LOCALITY: Bang 80, 111, 129 (BM).

NOMENCLATURAL COMMENTS: The herbarium name "bradeorum" was applied by Hieronymus to some specimens of S. popayanensis collected by the

Brade brothers in Costa Rica. This name, however, was apparently never published.

Alston et al. (1981) treated S. moritziana Spring var. pseudapoda A. Braun, as conspecific with S. popayanensis. I refer var. pseudopoda to S. moritziana, which see.

TAXONOMIC DISCUSSION: This species has been much confused. Alston (1952), Fraile (in Fraile et al., in press), and Stolze (1983) referred many of the specimens of S. popayanensis here cited to S. porphyrospora A. Braun, mostly because the lateral leaves usually possess short hairs on the upper surface near the basiscopic margin. Selaginella popayanensis is easily distinguished from S. porphyrospora by lacking (vs. having) "false veins" on the surfaces of the lateral leaves, deep orange (not reddish) microspores, and acute (not acuminate) lateral leaves.

Specimens referred to as S. anisoclada seem to be only a teratological development of S. popayanensis. Frequently, their leaves and stem at the terminal portion of the branches are compressed in such a way that they resemble propagules in the form of buds. This condition is frequently observed in S. porphyrospora where the buds are rounded, well differentiated from the subtending branch apex, and connected to it by a flagelliform elongation. These buds are, presumably, a mechanism that helps in the dispersion and generation of new plants. In describing S. anisoclada Crabbe & Jermy (1976) reported vegetative

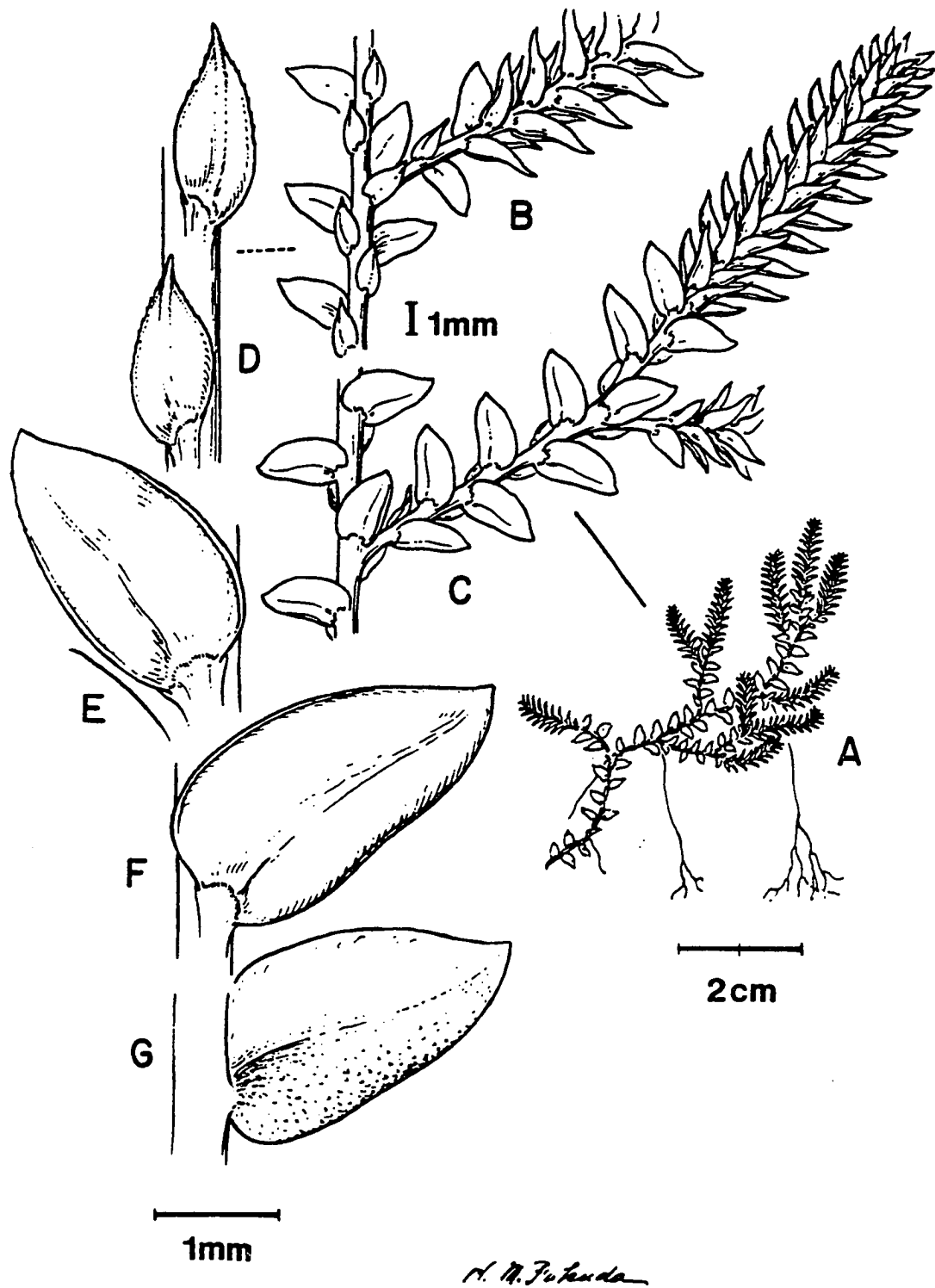
development from strobili tips, and almost isomorphic median and lateral leaves on ultimate branches. The vegetative growth from the strobilus tips is in the form of the already described "propagules," while the "almost isomorphic median and lateral leaves" seem to be due to the late development of arrested branch buds producing pseudoisomorphic lateral and median leaves.

Megaspores from the type collection of S. popayanensis differ slightly from those of the type collection of S. disticha in that both their proximal and distal face are somewhat more corrugate. This difference may be due to the developmental stage and age of the spores of S. popayanensis or it may indicate variation within the species. A more thorough study of spore morphology involving several populations would be desirable in order to assess these possible explanations for spore variation.

Selaginella popayanensis is closely related to a group of species including S. moritziana, S. cavifolia, and S. flacca.

Specimens from Ecuador [Wiggins 10637 (DS, UC, US) and Benoist 2700 (BM, P)] and one from Colombia [Pinto & Bichler 3516 (BM, COL)], cited by Alston et al. (1981) as S. popayanensis, are actually S. cavifolia. Therefore, S. popayanensis is, at least provisionally, excluded from Ecuador. Another collection from Colombia, Joseph s.n. (BM), also cited by Alston et al. (1981) as S. popayanensis, is S. moritziana.

Fig. 13. A-G. Selaginella popayanensis (Mickel 4295, NY). A. Habit. B. Upper surface of branch, with strobilus. C. Lower surface of branch, with ventral side of the strobilus. D. Median leaves. E. Axillary leaf. F. Lateral leaf, lower surface. G. Lateral leaf, upper surface.



**15. *Selaginella moritziana*** Spring, Mém. Acad. Roy. Sci. Belgique 24: 249. 1849.

Type: VENEZUELA. MÉRIDA: Moritz 377 (Holotype: B-n.v.; isotypes: BM!, G!, K-2 sheets!, LG!, P!). (Fig. 1A).

*Selaginella moritziana* Spring ex Klotzsch, Linnæa 20: 436. 1847, nom. nud.

Plants terrestrial or epipetric. Stems creeping or ascending to suberect, stramineous to greenish, 8-22 cm long, 0.4-0.8 mm diam., not articulate, not flagelliform, stoloniferous or not, 2- or 3-branched. Rhizophores axillary, throughout, or restricted to basal  $\frac{1}{2}$  or  $\frac{1}{4}$ , or to of the stem, filiform to stout, 0.08-0.2 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to rounded cells with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem or ascending, ovate to ovate-oblong,  $2.5-3.3 \times 1.2-1.9$  mm, base rounded, the acroscopic base usually strongly or slightly overlapping the stem, the basiscopic base not overlapping the stem, margins hyaline, the acroscopic margin serrate, or infrequently ciliate-denticulate along basal  $\frac{1}{3}$ , serrulate along apical  $\frac{2}{3}$ , the basiscopic margin serrulate apically, otherwise entire, both margins frequently with stomata; apex acute or short- to long-acuminate, denticulate at tip; the upper surface frequently hispid near the basiscopic margin, with or without idioblasts, without stomata, the lower surface glabrous, with conspicuous idioblasts, and with stomata along midrib. Median leaves distant, ascending, broadly ovate, ovate-deltate, or ovate-orbicular,  $1.2-2 \times$

0.68-1.2 mm; base asymmetric, oblique, or subcordate, the outer base frequently tufted with short hairs; the inner margin hyaline, serrate throughout or serrate basally and ciliate-denticulate apically, the outer margin greenish along basal  $\frac{1}{2}$ , hyaline along apical  $\frac{1}{2}$ ; apex short- to long-acuminate, or aristate, the acumen or arista  $\frac{1}{4}$  or less the length of the lamina, 0.1-0.36 mm long, dentate at tip, both surfaces glabrous, the upper surface usually with conspicuous or inconspicuous idioblasts, or these absent, with stomata along midrib, and along basal  $\frac{1}{2}$  of outer margin, the lower surface without stomata. Axillary leaves similar to lateral leaves, except the margins minutely serrulate basally, entire apically. Strobili terminal on branch tips and main stem apex, lax and flattened, dorsiventral, 2-8 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along  $\frac{2}{3}$  or completely along sporophyll length, asymmetric or ovate-lanceolate,  $1.45-1.9 \times 0.45-0.85$  mm, with a strongly developed and entire to denticulate keel along midrib, the base rounded, the margins hyaline, serrate, the apex short- to long-acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with or without idioblast, and with stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis without an adaxial flap, ovate to ovate-lanceolate,  $1.25-1.9 \times 0.58-0.86$  mm, with a slightly developed denticulate to entire keel along midrib, the base rounded, the

margins hyaline, serrulate, the apex acute or short- to long-acuminate, both surfaces composed of elongate cells with sinuate walls, glabrous, with obscure idioblasts, the stomata present only on the lower surface. Megasporangia in two ventral rows; megaspores orange-buff, light orange-yellow, or deep chrome (light orange to orange), frequently with a prominent equatorial flange, the proximal face reticulate-striate or corrugate-reticulate with open to close reticulum of moderately high ridges, the distal face reticulate or reticulate-corrugate with open reticulum of high ridges, 270-367  $\mu\text{m}$  diam. Microsporangia in two dorsal rows or absent from it; microspores not studied.

HABITAT AND DISTRIBUTION: In moist and mossy, cloud forests, in marshy meadows, on moist soil, on steep forested slopes, pastures, waterway- and road banks, on wet mossy rocks, near waterfalls; 1100-3200 m; Mexico, Guatemala, Honduras, Costa Rica, Panama, Colombia, Venezuela, Ecuador, and Peru.

NOMENCLATURAL COMMENTS: Badré (1983) cited Moritz 377 at LG as holotype of S. moritziana. This is erroneous since in the original protologue Spring (1849) cited only the collection at "H. Berol." (B).

There are four syntypes of S. moritziana var. suberecta A. Braun at B, all annotated by Braun. Two bear the collection number Hoffmann 84 and the other two Hoffmann 609. Each of them, however, has a different collection date. I have chosen "8 [Aug] 1855, Hoffmann 84" as the lectotype.



In the case of S. moritziana var. elongata A. Braun, I have chosen the specimen at G of Fendler 323 annotated by Braun as the lectotype. On this sheet, there appear to be two fragments, probably from the same collection; the small one near the upper right corner of the sheet bears Braun's annotation slip, and at the end of it Braun wrote the collection numbers 322 & 323. Among the isosyntypes at BR, G, GH, and K, there are some more compact, chartaceous, and yellowish fragments that match exactly Fendler s.n., the type of S. moritziana var. conferta. Thus, these isosyntypes may be mixed collections, including fragments of the type of var. conferta.

TAXONOMIC DISCUSSION: Selaginella moritziana is usually characterized by the presence of obscure to very conspicuous idioblasts on the upper surface of median leaves, dorsal sporophylls, and occasionally on lateral leaves, by conspicuous or not, short, submarginal hairs on the upper surface of the lateral leaves near the basiscopic margin, by the median leaves with the inner margin hyaline throughout, composed of elongate cells, serrate basally to serrulate apically, with the outer margin hyaline along apical half, composed of elongate cells, greenish along the basal half, composed of  $\pm$  polygonal to rounded cells, with stomata throughout it. Selaginella moritziana varies in the following characteristics: habit, shape of lateral and median leaves, presence of idioblasts on the upper surface of the leaves and sporophylls, presence of submarginal hairs on the upper surface of the lateral leaves, and on the length of leaf apices.

Selaginella moritziana as treated here is composed of three varieties. I have retained one of the varieties originally proposed by Braun (1865), var. elongata. Another of Braun's varieties, var. laxa, I consider conspecific with S. flacca Alston. In addition, I propose a new variety, var. pearcei (Baker) Valdespino, **comb. et stat. nov.**, to accommodate S. pearcei Baker, and S. oligoclada Baker, which I do not consider distinct enough from S. moritziana to warrant species recognition. Previously, Alston et al. (1981) synonymized S. oligoclada under S. pearcei. Another of the varieties proposed by A. Braun, S. moritziana var. pseudopoda, is doubtfully included within S. moritziana. Certainly, it is not S. popayanensis as proposed by Alston et al. (1981). The type collection of this variety is a delicate plant, which I believe best to be regarded as a form of S. moritziana.

The varieties here proposed were recognized in an attempt to provide the means to distinguish some populations that share some characters making them consistently distinct. These characters, however, are considered non-fundamental and, moreover, do not show a distinct correlation with geographic patterns. Nevertheless, at the present time I consider it constructive to highlight the differences encountered in these populations so that future research can be carried out, in order to determine whether or not they are the result of environmental factors, such as light intensity (e.g., in páramo or roadbank habitats), humidity, or substrate, or if they have a genetic basis.

Key to the taxa in the S. moritziana complex

1. Upper surface of median leaves smooth; median and lateral leaves without idioblasts on the upper surface; upper surface of lateral leaves glabrous or hispid near the basiscope margin.
  2. Median leaves ovate, the inner margin curved, the apex acute to shortly acuminate; upper surface of dorsal sporophylls without idioblasts; lateral leaves broadly ovate or broadly ovate-elliptic, the apex obtuse, to broadly acute, or occasionally abruptly acute, the upper surface glabrous.....17. S. cavifolia
  2. Median leaves elliptic to ovate-elliptic, the inner margin tending to be straight, the apex long-acuminate to aristate; upper surface of dorsal sporophylls usually with idioblasts; lateral leaves ovate-elliptic or ovate-oblong; the apex short- to long-acuminate, the upper surface frequently with short hairs near basiscope margin.....16. S. flacca
1. Upper surface of median leaves rugose to rugulate or irregularly smooth, if the latter then with conspicuous idioblasts; median and lateral leaves with conspicuous or inconspicuous idioblasts on the upper surface; upper surface of the lateral leaves frequently with conspicuous or inconspicuous, short hairs near the basiscope margin.
  3. Stems creeping, without stolons at the base; rhizophores borne throughout or at least along basal half of the stem; upper surface of

median leaves and frequently of lateral leaves with conspicuous idioblasts, the idioblasts frequently aggregated to form patches; lateral leaves lanceolate to lance-ovate, or ovate-elliptic.....

.....15b. S. moritziana var. elongata

3. Stems ascending to suberect, with stolons at the base; rhizophores

restricted to basal  $\frac{1}{4}$  of the stem; upper surface of median leaves with conspicuous or inconspicuous idioblasts, that of lateral leaves with or without idioblasts, the idioblasts not forming distinct patches; lateral leaves broadly ovate, broadly or narrowly ovate-elliptic, or ovate-oblong.

4. Upper surface of median leaves, dorsal sporophylls, and

infrequently lateral leaves with conspicuous idioblasts, the idioblasts elongate; upper surface of lateral leaves usually with short, submarginal hairs near basiscopic margin; median leaves with outer base frequently tufted with short hairs.....

.....15c. S. moritziana var. pearcei

4. Upper surface of median leaves, dorsal sporophylls, and

infrequently lateral leaves with inconspicuous idioblasts, the idioblasts short; upper surface of lateral leaves glabrous or with very inconspicuous hairs near basiscopic margin; median leaves with outer base glabrous.....

.....15a. S. moritziana var. moritziana

**15a. *Selaginella moritziana* Spring var. *moritziana***

*Selaginella moritziana* Spring var. *normalis* A. Braun, Ann. Sci. Nat. Bot. V, 3:

284. 1865, nom. nud.

*Selaginella moritziana* Spring var. *pseudapoda* A. Braun, Ann. Sci. Nat. Bot. V, 3: 285. 1865.

Type: COLOMBIA. [CUNDINAMARCA]: Manzanos, 2700 m [not 1700 m], Jul 1860, Lindig 1518 (Holotype: presumably B-n.v.; isotypes: BM!, K!, P!).

*Selaginella moritziana* Spring var. *suberecta* A. Braun, Ann. Sci. Nat. Bot. V, 3: 285. 1865.

Type: COSTA RICA. [HEREDIA]: Volcán de Barva, 8 [Aug] 1855, Hoffmann 84 (Lectotype: B!, here designated; isoelectotype: B!). Other syntype: COSTA RICA. Aguaiate [Aguacate?], Hoffmann 609 (B-2 sheets!).

This variety is characterized by the syndrome of characters provided above in the key.

HABITAT AND DISTRIBUTION: In cloud, mossy forests, in marshy meadows, on steep forested slopes, pastures, waterway- and road banks, or on wet mossy rocks; 1100-3200 m; Mexico, Guatemala, Honduras, Costa Rica, Panama, Colombia, Venezuela, and Ecuador.

COMMON NAME: Ciprés rastrero (Widmer 222).

SPECIMENS EXAMINED: MEXICO. CHIAPAS: Chamula, Paraje of Muk'inha (Las Ollas), near Chamula boundary with Tenejapa, 2713 m, 13 Jul 1981, Breedlove 51445 (CAS); El Porvenir, NW slope of Cura Malé, 3-4 km W of El Porvenir along road from Huixtla to Siltepec, 2800 m, 26 Nov 1981, Breedlove & Bartholomew 55973 (CAS); Siltepec, above Siltepec on the road to Huixtla, 2000-2400 m, 18 Jan 1973, Breedlove & A. R. Smith 31859 (DS, F, MICH-2 sheets, NY); Tenejapa, near Paraje Banabil, 2713 m, 8 Oct 1981, Breedlove 53366 (CAS), 2680 m, 12 Jan 1982, Breedlove 57070 (CAS); Unión Juárez, SE side of Volcán Tacaná above Talquian, 2700 m, 5 Mar 1972, Breedlove 24378 (DS).

GUATEMALA. SAN MARCOS: Volcán Tacaná, along Quebrada Canjulá, between Sibinal and Canjulá, 2200-2500 m, 18 Feb 1940, Steyermark 36012 (F, US); between town of Tajumulco and Tecutla (9 mi S of and W of Tajumulco), northwestern slopes of Volcán Tajumulco, 1800-2500 m, 27 Feb 1940, Steyermark 36824 (F, US); along road above Barranco Eminencia, ca. 2700 m, 14 Mar 1939, Standley 68480 (F); Barranco Eminencia, road between San Marcos and San Rafael Pie de la Cuesta, between Finca La Lucha and Buena Vista, 2500-2700 m, 6 Feb 1941, Standley 86206 (F, US), 86390 (US), 86431 (US), 86452 (F, US); near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, 1800-2400 m, 10-18 Dec 1963, L. O. Williams et al. 25737 (F, NY, US, W), L. O. Williams et al. 25802 (BM, DS, F, GH, NY, US, W).

HONDURAS. FRANCISCO MORAZÁN: Montaña La Tigra, Vuelta de La Matraca N of San Juancito, 2000 m, 24 Mar 1957, Molina 7771 (F, GH, NY, US-2 sheets); Montaña La Tigra, 2200 m, 8 Mar 1962, Molina 10259 (F, NY, US, W), 10295 (US).

COSTA RICA. ALAJUELA: L'Achiote, Volcán Poás, 2200 m, Nov 1896, Tonduz 10694 (G-5 sheets, M, P, US), Tonduz 10696 (US); vicinity of Fraijanes, 1500-1700 m, 12-13 Feb 1926, Standley & Torres 47489 (US); San Carlos, 16 Aug 1940, Roig 4 (CR, F); Volcán Poás, Hacienda El Tirol, 2000 m, 6 Jul 1967, Mickel 2452 (NY). CARTAGO: Cerro Cuericí, 2950 m, 17 Aug 1988, Widmer 222 (Z); slope behind La Georgina, 3200 m, 14 Jun 1967, Hauke 438 (NY); Cerro de la Muerte, 1 km NW of Villa Mills, behind Hotel La Georgina, 2900 m, 8 Aug 1967, Mickel 3195 (NY, US); Cerro de La Muerte, "Madre Selva," 24.5 km NW of La Asunción, near km 67 on Interamerican Hwy, 2550 m, 11 Aug 1967, Mickel 3301 (NY, US); Orosi, 1100 m, 15 Mar 1932, Kupper 785 (M); Volcán Irazú Hwy, ca. 10000 ft [3050 m], 6 Jul 1961, Brown CR-18 (US); 2 km N of Hwy 8 on road to San Gerardo, N slope of Volcán Irazú, 9°59'N, 83°51'W, 2900 m, 17 Mar 1986, Yatskievych & McCrary 86-24 (MO); Volcán de Turrialba, Jan 1899, Pittier 14140 (P); southern slope of Volcán de Turrialba, near the Finca del Volcán de Turrialba, 2000-2400 m, 22 Feb 1924, Standley 35029 (BM, US), 35046 (US), 35151 (BM, US). HEREDIA: Volcán de Barva, 8 [Aug] 1855, Hoffmann 84 (B-2 sheets, lectotype coll. of S. moritziana var. suberecta); southwestern slope of Volcán Barva, above Sacramento, 10°7'-10°8'N, 84°7'-84°8'W, 2200-2300 m, 3 Feb

1982, Burger et al. 11443 (F); [Volcán] Barva, 2500 m, 6 Feb 1890, Tonduz 1908 (BR, CR, P, US, Z); Volcán de Barva, 3 Feb 1935, Valerio 2362 (US); southern edge of Parque Nacional Braulio Carrillo, above Sacramento and San José de La Montaña, 2500-2700 m, 24 Jul 1980, Wilbur 29594 (US); Río Ciruelas, S slope of Volcán Barva, at end of Rte. 114, 7.5 km N of San José de La Montaña (ca. 1 km N of Porrosatí), 30 Mar 1973, Stolze 1584 (F, US), 1597 (CR, F, US); 10-12 km N of San Rafael, ca. 1 km N de la entrada de la Reserva Biológica Chompipes, 1700-1800 m, 1 Dec 1991, Valdespino 1278 (CR, NY, PMA), 12 Dec 1991, Valdespino 1294 (CAS, CR, BM, HUA, F, MEXU, MICH, MO, NY, PMA, UC, US), 1300 (B, CR, F, NY, P, PMA, UC); N of Heredia, ca. 1 km beyond Porrosatí, 2100 m, 18 Aug 1970, Lellinger & White 1684 (CR, F, US); along Vara Blanca (between Poás and Barva volcanoes) to La Concordia, 1600-1950 m, 23 Jul 1923, Maxon & Harvey 8463 (MICH, US). LIMÓN: Cordillera de Talamanca, Atlantic slope, S side of unnamed cordillera between Río Terbi and Río Siní, 2-4 airline km W of Costa Rican-Panamanian border, 9°9'-09°11'N, 82°58'W, 2300-2500 m, 11 Sep 1984, Davidse et al. 28951 (CR, UC). PUNTARENAS-LIMÓN: Cordillera de Talamanca, continental divide halfway between Cerro Dudu and Cerro Nai, 9°13'30"N, 83°05'W, 2850 m, 26 Mar 1984, Davidse et al. 26094 (CR, UC). SAN JOSÉ: Cerro de la Muerte, ca. 10 mi above Empalme, 20 Nov 1973, McAlpin 2395 (US); near Finca La Cima, above Los Lotes, N of El Copey, 2100-2400 m, 21-22 Dec 1925, Standley 42644 (BM, US); Las Nubes, 1500-1900 m, Standley 38554 (US). WITHOUT SPECIFIC PROVINCE: Aguaiate [Aguacate?],



Hoffmann 609 (B-2 sheets, syntype coll. of S. moritziana var. suberecta).

PANAMA. CHIRIQUÍ: Bugaba, above Cerro Punta, ca. 2 mi E of Guadalupe, along Río Chiriquí Viejo, 24 Jul 1972, McAlpin 1449 (CAS, F, US); Bugaba, Cerro Punta, camino hacia la antigua cabaña de STRI, Parque Nacional de La Amistad, ca. 2000 m, 2 Jan 1992, Valdespino et al. 1327 (B, CAS, CR, HUA, NY, PMA, QCA, UC, US); Bugaba, Cerro Punta, 8°52'N, 82°33'W, 2200 m, 24 Jan 1985, van der Werff & Herrera 6346 (GH, UC, US).

COLOMBIA. [CUNDINAMARCA]: Manzanos, 2700 m [not 1700 m], Jul 1860, Lindig 1518 (B-n.v., BM, K, P, type coll. of S. moritziana var. pseudopoda).

VENEZUELA. MÉRIDA: Moritz 377 (B-n.v., BM, G, K-2 sheets, LG, P, type coll. of S. moritziana var. moritziana).

ECUADOR. MORONA-SANTIAGO: trail Alao-Huamboya, around and above El Placer, 1°47'S, 78°23'W, 8 May 1982, Øllgaard et al. 38403 (AAU). PICHINCHA: western declivity of [Volcán?] Pichincha, Jameson (K).

**15b. *Selaginella moritziana* Spring var. *elongata* A. Braun, Ann. Sci. Nat. Bot. V, 3: 285. 1865.**

Type: VENEZUELA. ARAGUA: Colonia Tovar, Fendler 323 (Lectotype: G!, here designated; isoelectotypes: BR!, G!, GH-2 sheets!, K!, MO!, NY!).

Other syntype: VENEZUELA. ARAGUA: Colonia Tovar, Fendler 322 (BM-n.v. [fide Alston et al., 1981: 286; Smith & Todzia, 1989:341.]). See

additional information on syntypes under "Nomenclatural Comments."

This variety is characterized by usually prostrate stem, dark green leaves, upper surface of both lateral and median leaves strongly covered with many idioblasts, the idioblasts may actually completely occupy part of the upper epidermis.

HABITAT AND DISTRIBUTION: : On wet forested slopes, on moist soil, waterway- and road banks, or mossy rock banks; 1280-3000 m; Colombia and Venezuela.

SPECIMENS EXAMINED: COLOMBIA. BOYACÁ: Sierra Nevada de Cocuy, ca. 2900 m, 16 Aug 1957, Grubb & Guymer P.57 (BM, US); Sierra Nevada de Cocuy, around Bocota, ca. 2200 m, 22 Aug 1957, Grubb & Guymer P.83 (BM, COL, US). NORTE DE SANTANDER: margen oriental de la carretera a Pamplona, 4200 ft [1281], 11 Nov 1978, Alvarez et al. 9 (COL). SANTANDER: Corcoba [La Corcova?], near Bucaramanga, 2450 m, 27 Feb 1939, Alston 7296 (BM); Río de La Baja, below La Baja, 2200-2300 m, 26 Jan 1927, Killip & A. C. Smith 18280 (NY); vicinity of La Baja, 3000 m, 14-31 Jan 1927, Killip & A. C. Smith 18348 (NY); Gámbita, carretera entre Duitama y Charalá, 2200 m, 19 Sep 1983, Santa & Buitrago 894 (AAU, COL); vicinity of Las Vegas, 2600-3000 m, 21-23 Dec 1926, Killip & A. C. Smith 16024 (NY).

VENEZUELA. ARAGUA: Colonia Tovar, Fendler 323 (BR, G-2 sheets, GH-2 sheets, K, MO, NY, lectotype coll. of S. moritziana var. elongata), Fendler 322 (BM-n.v. [fide Alston et al., 1981: 286; Smith & Todzia, 1989:341.], syntype coll. of S. moritziana var. elongata). TÁCHIRA: Junín, La Esplanada del Peligro, S of Betania, adyacente al Páramo Tamá, 2500 m, Aug 1980, Delascio & Mondolfi 9127 (UC); along Quebrada Agua Azul, S of El Reposo, 14 km SE of Delicias, 7°31'N, 72°24'W, 2150-2300 m, 22-23 Jul 1979, Steyermark & Liesner 118332 (UC), 118414 (MO, UC).

NOMENCLATURAL COMMENTS: I have determined that one of the original collections cited by A. Braun (1865) when describing var. elongata, Lindig 1505 (BM!, GH!, K!, P!), is conspecific with S. cavifolia. Therefore, it has been excluded from var. elongata. I have lectotypified S. moritziana var. elongata based on Fendler 323 as submitted in the preceding synonymy. Additional discussion on the status of var. elongata is found under S. cavifolia.

**15c. *Selaginella moritziana* Spring var. *pearcei* (Baker) Valdespino, comb. et stat. nov.**

*Selaginella pearcei* Baker, J. Bot. 22: 246. 1884.

Type: PERU. [Huánuco]: Cordillera of Pozuzo, 6000 ft [1830 m], 1863,

Pearce 249 (Holotype: K!, fragment B!).

Selaginella oligoclada Baker, J. Bot. 22: 277. 1884.

Type: NEW GRANADA [COLOMBIA. NORTE DE SANTANDER]: Ocaña to Pamplona, 8300 ft [2531 m], 3 Apr 1879, Kalbreyer 1080 (Holotype: K!, fragment B!; isotype: B!).

Plants of this variety are more robust with a larger and wider, ascending to suberect stem, the leaves are dark to light green, chartaceous and shiny, frequently the epidermis of the upper surface of the leaves has conspicuous elongate idioblasts, the lateral leaves are usually narrowly ovate to narrowly ovate-elliptic with a long-acuminate apex, with the upper surface having short submarginal to marginal hairs near the basiscopic margin, the median leaves are ovate-lanceolate to broadly ovate with a long-acuminate to short-aristate, or infrequently long-aristate apex, and with a ventricose to subventricose, outer base that is frequently tufted with short hairs.

HABITAT AND DISTRIBUTION: In moist cloud forests; on roadside- and waterway banks, on rocks in moist ravines, on mossy rocks, or near waterfalls; 1830-3200 m; Costa Rica, Colombia, Venezuela, Ecuador, and Peru.

SPECIMENS EXAMINED: COSTA RICA. CARTAGO-SAN JOSÉ: Slopes at La Sierra near km 44, ca. 25 km S of the intersection of the Cartago-San José Hwy and the Interamerican Hwy, 1950 m, 23 Jul 1980, Wilbur 29529 (US).

COLOMBIA. CAUCA: Above Carpinteria, eastern slopes, 2500 m, 23 Apr 1939, Alston 8217 (AAU, BM, COL, US); W slope of Cordillera Occidental, W of Tambo, 2500 m, Haught 5209 (US); SW slope of Cerro Munchique, 40 km W of Popayán, 2400-2500 m, 6 Oct 1961, R. Tryon & A. Tryon 5999 (US); W Andes of Popayán, 2600-3000 m, Mar, Lehman 6969 (K-2 sheets, US). MAGDALENA: Mts. above hacienda Cincinnati, Santa Marta, 7000 ft [2135 m], 4 Aug 1946, M. Foster & E. Smith 1392 (A, COL).

VENEZUELA. MÉRIDA: Andrés Bello, Zerpa, La Carbonera, 3 Mar 1982, Marin et al. 135 (F); Andrés Bello, La Carbonera, 2500 m, 3 Mar 1982, Ricardi 135 (F); Sierra Nevada, 2800 m, 2 Feb 1939, Alston 6779 (AAU, BM, MG, NY, QCA). TRUJILLO: Mts. above San Rafael de Boconó, 2500 m, 3 Apr 1947, Box 3830 (BM); 9 km from San Rafael, entre Trujillo y Boconó, entre Urbina y San Rafael, 2300-2500 m, 3-4 Sep 1966, Steyermark & Rabe 97283 (GH, K).

ECUADOR. LOJA: Parque Nacional Podocarpus, trail Cajanuma-Laguna de Compadres, 2750-3200 m, 26 Dec 1988, Jørgensen et al. 65666 (AAU); Parque Nacional Podocarpus, above Nudo de Cajanuma, 4°05'S, 79°10'W, 2850-3050 m, 25-26 May 1988, Øllgaard et al. 74478 (AAU); Parque Nacional Podocarpus, on road Yangana-Cerro Toledo, 4°23'S, 79°08'W, 2600-2800 m, 3 Jun 1988, Øllgaard et al. 74627 (AAU). LOJA-ZAMORA-CHINCHIPE: Road between Loja and Zamora, ca. km 9, 2500-2750 m, 31 Dec 1978, Luteyn et al. 6561 (AAU, NY). ZAMORA-CHINCHIPE: Limit of Parque Nacional Podocarpus, new road Loja-Zamora, E of the pass, 3°58'S, 79°07'W, 2500-3000 m, 25 Mar 1990, Madsen 87089 (AAU); 5 km

S of summit on Yangana-Valladolid road, ca. 25 km S of Yangana, 2615 m, 7 Jul 1989, Valdespino & Dorr 1065b (NY); 11.6 km S of summit on Yangana-Valladolid road, 2400 m, 8 Jul 1989, Valdespino & Dorr 1073 (NY).

PERU. HUÁNUCO: Cordillera of Pozuzo, 6000 ft [1830 m], 1863, Pearce 249 (K, fragment B, type of S. pearcei). JUNÍN: between San José and La Achira, Montañas de Pangoa, Raimondi 1563 (BM). WITHOUT SPECIFIC DEPARTMENT OR LOCALITY: Peruvian Andes, 1836, Matthews (BM).

TAXONOMIC DISCUSSION: Selaginella pearcei, which is considered here a variety of S. moritziana, has been synonymed by R. Tryon and Stolze (1994) under S. novae-hollandiae. Selaginella moritziana var. pearcei is not closely related to S. novae-hollandiae and can be easily distinguished from it by its median leaf bases not auricled (vs. with at least a conspicuous and free from the stem, outer auricle), the lateral leaves with the acroscopic margin frequently serrate to serrulate (vs. long-ciliate along basal  $\frac{1}{2}$  to  $\frac{3}{4}$ ), the axillary leaves serrulate basally and entire apically (vs. long-ciliate at least along basal  $\frac{1}{2}$  to  $\frac{3}{4}$ ), and orange-buff, light orange-yellow, or deep chrome (vs. snow- to bone-white or light cream) megaspores.

The following specimens could not be placed with certainty in any of the varieties because they were either depauperate or too young. They were identified only as S. moritziana.

SPECIMENS EXAMINED: COLOMBIA. ANTIOQUIA: Urrao, Encarnación, sitio El Río, 1 hr de camino del Páramo de Frontino, 6°27'N, 76°46'W, 3120 m, 7 Apr 1989, Callejas 7798 (NY, PMA). NORTE DE SANTANDER: Pamplona, 1911, Bro. Ariste-Joseph (BM, US); Ocaña to Pamplona, 10000 ft [3050 m], 1 Sep 1878, Kalbreyer 750 (K), 27 Dec 1878, Kalbreyer 894 (K).

VENEZUELA. BARINAS: Bolívar, entre Santo Domingo y Altamira, Quebradón, 1300-1500 m, 24 Nov 1984, Ortega & van der Werff 2368 (UC). TÁCHIRA: Lobatera, La Cazadora, 7°55'N, 72°18'W, ca. 1600 m, 24 Jul 1983, van der Werff & R. Ortíz 5637 (MO, UC).

PERU. SAN MARTÍN: Mariscal Cáceres, Parque Nacional Río Abiseo, Puerta del Monte, 3350 m, 13 Mar 1988, León & Young 1505 (BM).

16. *Selaginella flacca* Alston in Alston et al., Bull. Brit. Mus. (Nat. Hist.), Bot. 9: 269. 1981.

Type: VENEZUELA. DIST. FEDERAL (not Miranda): Quebrada Sebucan, prope Caracas, Ernst 1765 (Holotype: BM!, photo NY!).

*Selaginella moritziana* Spring var. *conferta* A. Braun, Ann. Sci. Nat. Bot. V, 3: 284. 1865.

Type: VENEZUELA. ARAGUA: Colonia Tovar, Fendler s.n. (Holotype: G!).

*Selaginella moritziana* Spring var. *laxa* A. Braun, Ann. Sci. Nat. Bot. V, 3: 284. 1865.

Type: VENEZUELA. [LARA: Barquisimeto], Karsten (Holotype: presumably B-n.v.; probable isotypes: F!, JE!, P!, W!).

Plants terrestrial or epipetric. Stems creeping or ascending, stramineous to greenish, 2.5-10(14) cm long, 0.08-0.5 mm diam., not articulate, occasionally flagelliform, stoloniferous, 1- or 2-branched. Rhizophores axillary, restricted to basal  $\frac{1}{2}$  or  $\frac{1}{4}$ , or throughout the stem, filiform, (0.06-)0.1-0.16 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of  $\pm$  polygonal to rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem or slightly ascending, ovate-elliptic or ovate-oblong,  $1.7-2.7 \times 1.1-1.4$  mm, base rounded, the acroscopic base slightly overlapping the stem, the basiscopic base not overlapping the stem, margins



hyaline, the acroscopic margin serrate, or infrequently ciliate-denticulate along basal  $\frac{1}{3}$ , serrulate along apical  $\frac{2}{3}$ , the basiscopic margin entire or serrulate apically, both margins frequently with stomata; apex short- to long-acuminate, denticulate at tip; the upper surface frequently hispid near the basiscopic margin or glabrescent, without idioblasts or stomata, the lower surface glabrous, with conspicuous idioblasts, and with stomata along midrib. Median leaves distant, ascending, ovate-lanceolate to lanceolate,  $0.9-1.7 \times 0.4-0.8(-0.92)$  mm; base asymmetric, oblique, or subcordate, the outer base subventricose, without hairs; the inner margin usually straight, hyaline, ciliate-denticulate or serrate, the outer margin greenish along basal  $\frac{1}{2}$ , hyaline along apical  $\frac{1}{2}$ , entire to serrulate apically; apex usually long-acuminate to aristate, the acumen or arista  $\frac{1}{4}$  or  $\frac{1}{3}$  the length of the lamina, 0.2-0.4 mm long, dentate at tip, both surfaces glabrous, the upper surface usually without idioblasts, with stomata along midrib and along basal  $\frac{1}{2}$  of outer margin, the lower surface without stomata. Axillary leaves similar to lateral leaves except the margins minutely serrulate on basal  $\frac{1}{3}$  to entire apically. Strobili terminal on branch tips and main stem apex, lax and flattened, dorsiventral, 2-10(-17) mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with an adaxial flap extending along  $\frac{1}{2}$  to  $\frac{3}{4}$ , or throughout the sporophyll length, asymmetric or lance-ovate,  $1.8-2.7 \times 0.6-0.94$  mm, with a strongly developed and denticulate keel along midrib, the base rounded, the margins hyaline, ciliate-denticulate, the apex short- to long-acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to

form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with or without idioblast, and with stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis without an adaxial flap, lanceolate to lance-ovate,  $1.6-2.0 \times 0.46-0.6(0.82)$  mm, with a slightly developed and denticulate keel along apical  $\frac{1}{2}$  of midrib, the base rounded, the margins hyaline, ciliate-denticulate, the apex usually long-acuminate to aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, with obscure idioblasts, the stomata present only on the lower surface. Megasporangia in two ventral rows; megaspores orange-buff, light orange-yellow, or deep chrome (light orange to orange), without an equatorial flange, the proximal face striate-corrugate to slightly striate-reticulate with slightly developed close to open reticulum of low ridges, the distal face reticulate-rugose to reticulate with open reticulum of low ridges, 250-280  $\mu\text{m}$  diam. Microsporangia in two dorsal rows or absent from it; microspores light orange, without an equatorial flange, the proximal and distal faces seemingly smooth, 19-20  $\mu\text{m}$  diam.

**HABITAT AND DISTRIBUTION:** In moist, cloud forests, on moist mossy rocks, steep and shaded banks, or on dry forested slopes; 1600-3100 m; Colombia and Venezuela.

SPECIMENS EXAMINED: COLOMBIA. ANTIOQUIA: Urrao, Páramo de Frontino, 3100 m, 18 May 1985, M. Escobar 20 (NY). CALDAS: Nevado del Ruíz, carretera Termales-Manizales, 2830 m, 20 Mar 1972, Cleef & Hart 2573 (COL). CUNDINAMARCA: eastern Cordillera, ca. 18 km NE of Fusagasugá, ca. 2500-2700, 26 Jun 1965, King & Guevara 5760a (US). SANTANDER: Bucaramanga, La Corcova, 2480 m, 22 Sep 1983, Santa & Buitrago 919 (AAU, COL); Corcoba [Corcova?], 2450 m, 27 Feb 1939, Alston 7293 (AAU, BM, QCA, US).

VENEZUELA. DIST. FEDERAL: Caracas, Moritz 71 (BM, E, K-2 sheets, P, W, not the type of S. lychnuchus var. flaccida); Galipán, Moritz 71 & 221 (BM, not the type of S. lychnuchus var. flaccida); Sierra de El Avila, 1600 m, 15 Dec 1938, Alston 5538 (BM); Cordillera del Avila, above Caracas, W of Los Flores, 1675 m, Steyermark 55135 (F, US); Silla de Caracas, Ernst 1567<sup>a</sup> (BM). MÉRIDA: Rangel, Quebrada La Virgen, 13.3 mi NW of La Soledad (Edo. Barinas), along road to Sto. Domingo, 8°52'N, 70°38'W, 1600 m, 19 Nov 1982, A. R. Smith et al. 1406 (MO, UC). MIRANDA: Parque Nacional El Avila, cabeceras de la Quebrada Chacaíto, quebrada que sigue a Lagunazo, 10°33'N, 66°51'W, 2020-2050 m, 2 Nov 1991, Meier 713 (UC); Parque Nacional El Avila, cabeceras de la Quebrada Chacaíto, 10°33'N, 66°52'W, 1995 m, 28 Feb 1992, Meier 1767 (UC). SUCRE: Helvetia, a orillas Amana, alrededores Turumiquiere, 1730 m, 26 Jan 1929, Nett 11 (BM). TÁCHIRA: Junín, southern slope of Cerro San Isidro, N of El Reposo, above hacienda Bella Vista, Quebrada Agua Caliente, 7°34'N, 72°25'W, 2000 m, 13-14 Nov 1982, Davidse & González 22134 (MO); Cabeceras del Río Quinimarí,

"Las Copas," al pié de la Peña de Pata de Judío (debajo del Páramo de Judío), 15 km al S de San Vicente de la Revancha, 30 km al S de Alquitrana, SW of Santa Ana, 2400 m, 10-11 Jan 1968, Steysmark & Dunsterville 1000549 (NY). WITHOUT SPECIFIC STATE OR LOCALITY: Moritz 71? (W, not the type of S. lychnuchus var. flaccida).

NOMENCLATURAL COMMENTS: It is possible that S. lychnuchus var. flaccida Spring may be conspecific with S. flacca. Unfortunately, I have not seen the holotype of var. flaccida, presumably at B, and am not sure of the true identity of its probable isotypes cited here under S. flacca (see discussion under S. lychnuchus). Therefore, var. flaccida has been provisionally cited in this monograph as a synonym of S. lychnuchus and not of S. flacca.

TAXONOMIC DISCUSSION: Selaginella flacca forms part of a difficult species complex centered around S. moritziana, including S. cavifolia. Some of the forms found in S. moritziana have been treated here as varieties. I recognize S. flacca as a separate species because the morphological characters and distribution pattern that separate it from the rest of the taxa in the complex are constant and do not intergrade with those of the other taxa examined.

Selaginella flacca is characterized by prostrate to ascending, slender stems, thin-textured leaves, with the upper surface without conspicuous idioblasts, the median leaves elliptic to ovate-elliptic, with the inner margin tending to be

straight, and with an aristate apex, the lateral leaves ovate-elliptic, and with a long-acuminate apex. It is mostly found at elevations above of 1900 m.

The type of S. flacca represents a very slender specimen, but it is otherwise similar to most of the specimens cited here. A specimen from Colombia, Santa & Buitrago 919, resembling S. flacca in having a long aristate median leaves, the lateral leaves with an acuminate apex, and the lack of conspicuous idioblasts on the upper surface of both leaves, is somewhat different from this species in having broadly ovate lateral and median leaves, and an overall robust appearance. Strobili examined from this collection were found to contain mainly abortive sporangia. It is not clear whether or not this specimen represents an intermediate form or a hybrid between S. flacca and S. moritziana. Until additional specimens can be examined and a more detailed study can be conducted, including field studies, I prefer to include this specimen within S. flacca.

Selaginella flacca may be confused with some slender specimens of S. cavifolia. E. Little & R. Little 9802, cited by Alston et al. (1981) as a paratype of S. flacca, is considered here to be S. cavifolia (which see for additional discussion).

17. *Selaginella cavifolia* A. Braun, Ann. Sci. Nat. Bot. V, 3: 272. 1865. (Figs. 3A-H).

Type: COLOMBIA. CUNDINAMARCA: Bogotá, Boquerón, 2700 m, Lindig 1511 (Lectotype: B!, here designated; isoelectotypes: BM!, K!, P!). Other syntype: COLOMBIA. CUNDINAMARCA: Salto de Tequendama, Triana (B!, BM!).

Plants terrestrial or epipetric. Stems creeping, stramineous to greenish, 4-10 cm long, 0.2-0.4 mm diam., not articulate, frequently flagelliform, not stoloniferous, 1- or 2-branched. Rhizophores axillary, throughout the stem, filiform, 0.06-0.18 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant to imbricate apically, perpendicular to the stem or slightly ascending, broadly ovate or broadly ovate-elliptic, (1.3-)1.5-1.8  $\times$  0.9-1.4 mm, base rounded, the acroscopic base strongly overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin pale green especially along basal  $\frac{1}{4}$  to  $\frac{1}{3}$ , serrate to serrulate, the basiscopic margin greenish, entire to sparsely serrulate, especially apically, both margins frequently with stomata; apex obtuse to broadly acute, or occasionally abruptly acute, denticulate at tip; the upper surface glabrous, without idioblasts or stomata, the lower surface glabrous, usually with or without conspicuous idioblasts, and with

stomata along midrib. Median leaves distant to slightly imbricate apically, ascending, ovate,  $0.9-1.42 \times 0.54-0.8$  mm; base asymmetric, oblique, or infrequently subcordate, the outer base subventricose, without hairs; the inner margin hyaline, serrate to serrulate, the outer margin greenish along basal  $\frac{1}{2}$ , hyaline along apical  $\frac{1}{2}$  in a band 3 or 4 cells wide with cells elongate, papillate, and with straight walls parallel to margin, serrate to serrulate; apex usually acute or shortly acuminate, the acumen less than  $\frac{1}{8}$  or  $\frac{1}{4}$  the length of the lamina,  $0.04-0.14(-0.2)$  mm long, dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib and frequently along basal  $\frac{1}{2}$  of outer margin, the lower surface without stomata and idioblasts. Axillary leaves similar to lateral leaves. Strobili terminal on branch tips, lax and flattened, dorsiventral, 2-6 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a slightly to strongly developed adaxial flap extending along  $\frac{1}{4}$  to  $\frac{3}{4}$  the sporophyll length, or sometimes ill-defined and absent, ovate to broadly ovate, or asymmetric,  $1-1.78 \times 0.5-1.12$  mm, with a slightly to strongly developed, entire to slightly denticulate keel along midrib, the base rounded, the margins pale green, sparsely serrulate to entire, or serrate, the apex acute to shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts, and with stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls hyaline to pale green, ascending,

pseudopeltately attached to the axis, without an adaxial flap, broadly ovate, 1.2-1.8 × 0.6-1.24 mm, with or without a slightly developed, entire keel along apical  $\frac{2}{3}$  of midrib, the base rounded, the margins hyaline to pale green, sparsely serrulate to entire, or serrate, the apex acute or occasionally shortly acuminate, both surfaces composed of elongate cells with sinuate walls, except lower surface (adaxial surface) with some rounded cells along apical  $\frac{1}{3}$ , glabrous, with obscure idioblasts, the stomata present only on the lower surface. Megasporangia in two ventral rows; megaspores capucine orange, pale yellow-orange, light orange-yellow, or orange-buff, usually without an equatorial flange or with a slightly developed one, the proximal face striate-reticulate to reticulate with close reticulum of rather low ridges, the distal face reticulate with open reticulum of high ridges, 300-362  $\mu\text{m}$  diam. Microsporangia in two dorsal rows; microspores not studied.

HABITAT AND DISTRIBUTION: On shady, humid river- or stream-banks, wet mossy rocks, roadbanks, or disturbed forest, usually in premontane forest or páramo; 2090-3680 m; Colombia, Venezuela, and Ecuador.

SPECIMENS EXAMINED: COLOMBIA. ANTIOQUIA: Carretera de San José de la Montaña hacia Toledo, Quebrada Santa Inés, 2660 m, 23 Oct 1980, Santa et al. 470 (COL, NY). CAUCA: Macizo Colombiano, páramo de Las Pampas, entre Boquerón y La Hoyala, 3200-3510 m, 7-27 Nov 1958; Idrobo et al. 3516 (BM, COL); Purace (km 6), 2750 m, 16 Apr 1939, Alston et al. 8063 (BM).



**CUNDINAMARCA:** Bogotá, near La Gruta, canyon E of Calle 57, 9000-9500 ft [2745-3035 m], 14 May 1944, E. Little & R. Little 7862 (COL, GH, US), 7863 (US); Bogotá, canyon at NE edge of Bogotá (E of Calle 72), 9000 ft [2745 m], 19 Mar 1945, E. Little & R. Little 9802 (GH, US); Bogotá to El Salto (Tequendama), falls of Río Bogotá, vicinity of El Salto, 8100-8300 ft [2470-2531 m], 18 May 1944, E. Little & R. Little 7897 (COL, GH, US); Bogotá, región de Monserrate, El Granizo, 3100 m, 13 Apr 1980, Zuluaga 195 (COL); Bogotá, Río Arz, 2900 m, May 1860, Lindig 1505 (BM, GH, K, P, syntype of S. moritziana var. elongata); Bogotá, Laches, 2800 m, Sep 1859, Herb. Triana [Lindig ?] (BM); [Bogotá], Salto de Tequendama, 2100 m, 8 Mar 1939, Alston 7413 (AAU, BM, COL, US-2 sheets); Cerro de Suba, extremo N, 2600 m, 14 Dec 1967, R. Jaramillo et al. 4615 (COL); Macizo de Bogotá, Quebrada de las Delicias, 2800-3000 m, 25 Jun 1939, Cuatrecasas 5600 (COL, US); páramo entre Cogua y San Cayetano, Laguna Verde y alrededores, 700 m al NW de la Laguna, 3680 m, 12 Nov 1972, Cleef 6275 (COL, U, US); Laguna de Chisacá, km 32 de la carratera, 3640 m, 20 Apr 1974, Acosta-Arteaga 309 (COL); páramo de Sumapaz, Chisacá, cabeceras del Río S. Rosa, ca. 1 km al S de la Laguna Larga, 3680 m, 22 Aug 1972, Cleef 5200 (COL).

**META:** Macizo de Sumapáz, alrededores de la Laguna La Guitarra, 3380-3420 m, 4 Jul 1981, Díaz 2413 (COL); páramo de Sumapaz, Hoya El Nevado, Laguna La Guitarra y alrededores, 3390 m, 23 Jan 1973, Cleef 8257 (COL, U); Sebastopol, 8000 ft [2440 m], 3 Sep 1944, E. Little & R. Little 8611 (US).

**NARIÑO:** entre La Victoria y el páramo El Consuelo, 2900 m, 12 Jan 1973, Hagemann & Leist 1927

(COL). NORTE DE SANTANDER: La Mesita, Pamplona, 2825 m, 20 Feb 1939, Alston 7191a (BM); La Mesita, Pamplona, 2825 m, 23 Feb 1939, Alston 7236 (AAU, BM, MG, NY, QCA, US).

VENEZUELA. TRUJILLO: Boconó, Páramo Guaramacal, 20-21 km beyond jct. with hwy. NE of Boconó, ca. 9°13'N, 70°13'W, 2640-2700 m, 14 Mar 1984, Luteyn & Cotton 9678 (NY), 9685 (NY-2 sheets).

ECUADOR. AZUAY: Cerro Urucaca, ca. 2 km S of Cumbe, S of Cuenca, 3°07'S, 79°01'W, ca. 3000 m, 30 Oct 1978, M. Lewis 78-2170 (F); Río Panjón, ca. 2 km NE of Sevilla de Oro, 2°48'S, 78°38'W, 2600 m, 19 Jun 1979, Løitnant et al. 15152 (AAU). BOLÍVAR: 5 km W of San Pablo, 1°49'S, 79°05'W, 2490 m, 24 Jun 1989, Valdespino & Dorr 1054 (NY). CARCHI: El Ajún, along road N of El Playón de San Francisco, towards El Carmelo, 0°42'N, 77°36'W, 10 Aug 1990, Øllgaard et al. 98133 (AAU); páramo El Angel, 13 km al N de El Angel, 0°38'N, 77°53'W, 3600 m, 29 Dec 1982, Balslev & de Vries 3618 (QCA); Tulcán-El Angel road, 15 km S of Las Juntas, 3300 m, 20 Nov 1980, Balslev & Quintana 831 (NY); SE slopes of Volcán de Chile, near village of Tufino, 10900 ft [3324 m], 17 Aug 1944, Wiggins 10637 (DS-2 sheets, UC, US-3 sheets). LOJA: S slopes of Cerro Villonaco, summit of Loja-Catamayo road, 4°00'S, 79°16'W, 2700 m, 18 Jun 1979, Løitnant et al. 15078 (AAU, QCA). MORONA-SANTIAGO: Area known locally as Aturaq, 17 km SW of Sigsig (Prov. Azuay), on road to Chiguinda, 3°12'S, 78°37'W, 2800 m, 20 Jun 1989, Valdespino & Dorr 1045 (NY). PICHINCHA: near Calacali, via Nanegal, 1600-2400 m, 1917, L. Mille (MO); Valley of Lloa (Ungü), 3 Jul 1930,

Benoist 2700 (BM, P); Lloa Valley, on Hcda. Las Palmas of Lcdo. Fernando Sotomayor, Lloa-Mindo, km 14, 0°10'S, 78°38'W, 2900 m, 8 May 1988, Jørgensen et al. 65331 (AAU); near Niebly [Nieblí?], 6 May 1872, Sodiro [2?] (AAU).  
**ZAMORA-CHINCHIPE:** Road between Loja and Zamora, Km 22-27, 2050-2250 m, 1 Jan 1979, Luteyn et al. 6632 (NY); slopes along Río Valladolid, between Quebrada Honda and Tambo Valladolid, 2000-3000 m, 12 Oct 1943, Steyermark 54584 (F, US); 11.6 km S of summit on Yangana-Valladolid road, 2400 m, 8 Jul 1989, Valdespino & Dorr 1074 (NY); banks of Río Zamora, ca. 25 km E of Loja on new road to Zamora, 2090 m, 11 Jul 1989, Valdespino & Dorr 1089 (NY).  
**WITHOUT SPECIFIC PROVINCE OR LOCALITY:** In silvis Subano?, 1872, Sodiro (K); in silvis Subano?, 9 Aug 1899, Sodiro (G, P); May 1872, Sodiro 191 (K); Sodiro (UC).

**NOMENCLATURAL COMMENTS:** As explained under S. moritziana var. elongata, one of its original collections, Lindig 1505, is actually S. cavifolia. Alston et al. (1981), probably based on this, treated S. moritziana var. elongata as a synonym of S. cavifolia and referred all its syntypes to the latter. In this monograph I have lectotypified var. elongata, based on Fendler 323, and believe, contrary to Alston et al. (1981), that this collection is not S. cavifolia but a variety of S. moritziana.

**TAXONOMIC DISCUSSION:** Selaginella cavifolia is typically characterized by

its broadly ovate lateral leaves with an obtuse to broadly acute apex, the median leaves with an acute to short-acuminate apex and a prominent midrib along the leaf length, the sporophylls broadly ovate, and compact, creeping habit. It belongs to the S. moritziana species complex. Among the taxa in this complex it is closely related to S. flacca. The two species are similar in leaf epidermal pattern. In fact, some specimens of S. cavifolia growing in shady, humid conditions tend to develop a more acuminate median and lateral leaf apex, a lax and creeping habit, and in general a more delicate texture, and therefore are difficult to separate from S. flacca (e.g., Alston 8063, E. Little & R. Little 8611, 9802, Valdespino & Dorr 1045, 1054, 1074, 1089).

Specimens of S. cavifolia with the previously mentioned characteristics can be distinguished from S. flacca by the apex of the lateral leaves usually abruptly acuminate (vs. gradually short to long-acuminate), both sporophylls, in general, broadly ovate (vs. lanceolate to lance-ovate), and the margins of the dorsal sporophylls usually pale green to obscurely hyaline (vs. conspicuously hyaline). One of these specimens, Valdespino & Dorr 1074, is particularly difficult to distinguish from S. flacca; it has lateral leaves gradually tapering into an acuminate apex, and the strobili possess totally abortive sporangia on the ventral side and seemingly abortive microsporangia on the dorsal side. The sporophylls, however, are typical of S. cavifolia. Since it is unclear whether this specimen represents a hybrid or a form of S. cavifolia, I prefer to treat it within S. cavifolia until additional studies can be conducted.

Selaginella cavifolia is easily distinguished from other species in the S. mortiziana complex by the absence idioblasts on the upper surface of the leaves, and broadly ovate lateral leaves.

**18. *Selaginella bernoullii* Hieronymus, *Hedwigia* 41: 192. 1902. (Figs. 7F-J; 14A-F).**

**Type:** GUATEMALA. **QUICHÉ:** between Cubulco and Joyabaj, Sep 1870, Bernoulli 1121 (Lectotype: B!, here designated; isoelectotypes: B!, K!, P! [on same sheet with Bernoulli & Cario 160]). **Other syntype:** GUATEMALA. **QUICHÉ:** between Cubulco and Joyabaj, Sep 1870, Bernoulli & Cario 160 (B-2 sheets!, P! [on same sheet with Bernoulli 1121]).

Plants terrestrial or epipetric. Stems suberect, stramineous or greenish, 9-25 cm long, 0.3-1 mm diam., not articulate, occasionally flagelliform, stoloniferous with tuber-like buds at the tip, 2- or 3-branched. Rhizophores axillary and dorsal or axillary-ventral and dorsal, restricted to basal  $\frac{1}{4}$  to  $\frac{1}{3}$  of the stem, filiform, 0.08-0.32 mm diam. Leaves dimorphic throughout or above basal  $\frac{1}{4}$ , membranous, the upper surface green, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem or slightly ascending, ovate, ovate-oblong, or semicordiform, 2.4-5  $\times$  1-2.4 mm, base rounded to semicordate, the acroscopic base strongly overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin hyaline, serrate to serrulate apically, the basiscopic margin pale green to hyaline, entire to sparsely serrulate, especially apically, the basiscopic margin frequently with stomata; apex acute, dentate at tip; the upper surface usually puberulent, especially near

basiscopic margin, without idioblasts or stomata, the lower surface glabrous, usually with conspicuous idioblasts, and with stomata along midrib. Median leaves distant to slightly imbricate apically, ascending, broadly ovate-elliptic,  $1.3-2.2 \times 0.7-1.2$  mm; base asymmetric, usually with the inner base truncate and the outer base decurrent, or oblique; margins hyaline, sparsely serrate; apex abruptly aristate, the arista  $\frac{1}{4}$  to  $\frac{1}{2}$  the length of the lamina, 0.3-1 mm long, puberulent and dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib and throughout the lamina mostly concentrated along both margins, particularly along basal  $\frac{1}{2}$  of outer margin, the lower surface without idioblasts and stomata. Axillary leaves similar to lateral leaves. Strobili terminal on branch tips, lax and flattened, dorsiventral, 2-6 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{1}{2}$  to  $\frac{3}{4}$  the sporophyll length, asymmetric or ovate to ovate-lanceolate,  $1.3-2.1 \times 0.45-1.2$  mm, with a strongly developed, denticulate keel along midrib, the base rounded, the margins hyaline, sparsely serrate to serrulate, the apex acute to shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, puberulent, without idioblasts, usually with conspicuous stomata throughout, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls hyaline to greenish-hyaline, ascending, pseudopeltately attached to the axis without an adaxial flap, ovate to ovate-

lanceolate,  $1.08-1.7 \times 0.44-0.78$  mm, with a slightly developed, denticulate keel along midrib, the base rounded, the margins hyaline, serrate to serrulate, the apex short to long-acuminate, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present only on the lower surface. Megasporangia few (1-3) at the base of ventral rows; megaspores cream, usually without an equatorial flange or with a slightly developed one, the proximal face rugulate to rugulate-reticulate with close reticulum of rather low height ridges, the distal face reticulate with open reticulum of low ridges, 250-300  $\mu\text{m}$  diam. Microsporangia in two dorsal rows or strobili almost wholly microsporangiate; microspores not studied.

HABITAT AND DISTRIBUTION: On wet and shady slopes and road banks, stream banks, or wet mossy rocks; 1372-3000 m; Mexico, Guatemala, Honduras, and El Salvador.

SPECIMENS EXAMINED: MEXICO. CHIAPAS: Cerro del Boquerón, middle region, Sep 1913, Purpus 6720 (US); NE of Cerro Boquerón on road from El Rosario to Niquivil, 2255 m, 29 Nov 1986, Breedlove & Sigg 66144 (CAS); Finca Yolanda, Aug 1913, Purpus 6721 (BM, GH, NY, UC, US); Jitotol, ca 12 km N of Jitotol, 2000 m, 28 Sep 1971, Breedlove 19967 (DS, MO, NY); Motozintla de Mendoza, 45-50 km NE of Huixtla along road to Motozintla, 1900 m, 17 Nov 1971, Breedlove & A. R. Smith 22688 (DS, NY), N and W slope of Cerro



Mozotal, along the road from Huixtla to El Porvenir and Siltepec, 3000 m, 18 Nov 1971, Breedlove & A. R. Smith 22825 (DS, NY), SW side of Cerro Mozotal, 11 km NW of the junction of the road to Motozintla along the road to El Porvenir and Siltepec, 2100 m, 19 Nov 1971, Breedlove & A. R. Smith 22847 (DS); near summit of Cerro Mozotal, 2750 m, 14 Oct 1980, Breedlove & Strother 46258 (CAS, ENCB, MO, NY); Siltepec, ridge above Siltepec on the road to Huixtla, 2000-2400 m, 18 Jan 1973, Breedlove & A. R. Smith 31894 (DS, NY); Unión Juárez, SE side of Volcán Tacaná above Talquian, 2700 m, 12 Nov 1972, Breedlove 29437 (DS, F, NY). OAXACA: Juquila, 42 km S of Juchatengo, 5100 ft [1555 m], 6 Jun 1972, Hellwig & Whitaker 1293 (MEXU, NY); Juquila, 48 km S of Juchatengo, 4500 ft [1372 m], 7 Jun 1972, Hellwig & Whitaker 1323 (MEXU); Juquila, 46 km S of Juchatengo, 4600 ft [1400 m], 7 Jun 1972, Hellwig & Whitaker 1327 (MEXU, NY); Juquila, 28-29 km N of San Gabriel, 4500-4700 ft [1372-1433 m], 10 Aug 1971, Mickel 6192 (NY); Pochutla, 181 km S of Oaxaca, 64 km N of Pochutla, 4500 ft [1372 m], 29 Sep 1970, Mickel 5092 (NY, UC).

GUATEMALA. ALTA VERAPAZ: Pansamalá, 3800 ft [1159 m], Apr 1889, J. D. Smith 1578 (K). CHIMALTENANGO: Near Tecpán, 2100 m, 22 Nov 1933, Skutch 699 (US). QUETZALTENANGO: Slopes of Volcán de Zumil, at and above Aguas Amargas, 2430-2850 m, 17 Feb 1939, Standley 65435 (F); Aguas Amargas, western slope of Volcán de Zunil, ca. 2450 m, 14 Jan 1941, Standley 83278 (F, US); Fuentes Georginas, western slope of Volcán de Zumil, ca. 2850, 4 Mar 1939, Standley 67471 (F); vicinity of Fuentes Georginas, slopes of Volcán de Zunil,

2300-2500 m, 3 Feb 1941, Standley 85940 (US). **QUICHÉ:** 25 mi E of junction with road to Chichicastenango along CA #1, 7600 ft [2318 m], 18 Jun 1972, Hellwig & Whitaker 1388 (NY); between Cubulco and Joyabaj, Sep 1870, Bernoulli 1121 (B-2 sheets, K, P, lectotype collection of S. bernoullii); between Cubulco and Joyabaj, Sep 1870, Bernoulli & Cario 160 (B-sheets!, syntype of S. bernoullii). **SAN MARCOS:** Sierra Madre Mountains, slopes of Cerro Tumbador, ca. 15 km W of San Marcos, 2600 m, 15 Dec 1962, L. O. Williams et al. 23099 (F, G-2 sheets, NY, S, US-2 sheets, W-2 sheets); W slope of Sierra Madre Mountains, near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, 1800-2400 m, 10-18 Dec 1963, L. O. Williams et al. 25363 (F, US), 25636 (GH, NY, W), 25826 (F, NY, US); Sierra Madre Mountains, ca. 6 km (airline) N of San Marcos, 2700 m, 13 Dec 1963, L. O. Williams et al. 25837 (DS, F, NY, S, US); Sierra Madre Mountains, slopes of Tajumulco Volcano, ca. 10 km W of San Marcos, 2400-2700 m, 3 Jan 1965, L. O. Williams et al. 27170 (BM, F, GH, NY, US, W). **SOLOLÁ:** Sierra Madre Mountains, near Nahuala, 2500 m, 17 Dec 1962, L. O. Williams et al. 23185 (F, NY, US-2 sheets, W), L. O. Williams et al. 23194 (F, G-3 sheets, NY, S, US-2 sheets, W-2 sheets).

**HONDURAS. LEMPIRA:** Celaque National Park, trail from Camp 1 to Río Naranjal, 14°33'N, 88°40'W, 2000 m, 14 Nov 1991, Moran 5548 (NY); Celaque National Park, between Camp 1 and first summit, ca. 8 km WSW of the town of Gracias, 14°33'N, 88°41'W, 2400 m, 18 Nov 1991, Moran 5642 (NY).

**EL SALVADOR.** Cerro El Pital, 2550 m, 16 Nov 1978, Seiler 733 (F, GH,

NY).

NOMENCLATURAL COMMENTS: Selaginella bernoullii has been repeatedly misunderstood by workers dealing with regional treatments of Selaginella for Mexico and Central America. Apparently, Alston (1955) was the first to synonymize it under S. porphyrospora, and subsequent authors (Gregory & Riba, 1979; Smith, 1981; Stolze, 1983), have followed his decision. None of them, however, examined type material. Mickel and Beitel (1988), having seen the two syntypes at B of S. bernoullii, correctly treated this species as distinct from S. porphyrospora. More recently, unfortunately, Fraile (in Fraile et al., in press) has again synonymized it under S. porphyrospora without studying type material. Fraile has completely misconstrued S. bernoullii, and annotated specimens belonging to it either as S. porphyrospora (e.g., Breedlove 29437, F; L. O. Williams et al. 27170, F) or S. cladorrhizans [= S. tenella] (e.g., Purpus 6721, BM; L. O. Williams et al. 25363, F). Upon examination of both syntypes of S. bernoullii, I agree with Mickel and Beitel (1988) in treating it as a distinct taxon, different from S. porphyrospora and not closely related to S. tenella. Further discussion on its separation from S. porphyrospora is presented below in the taxonomic discussion.

TAXONOMIC DISCUSSION: The puberulent lateral leaves (easily overlooked) distinguish S. bernoullii from all others with serrate median leaves except for S.

minima, S. moritziana, S. porphyrospora, and S. popayanensis. Selaginella popayanensis differs from S. bernoullii by its acute to gradually acuminate median leaves with conspicuous stomata only along the midrib. Selaginella bernoullii is similar to S. porphyrospora because of its puberulent upper surface of lateral leaves and upper sporophylls, abruptly aristate median leaves, and, frequently, with tubers at the base of the upright stems. It can be distinguished, however, by lack of false veins on the upper surface of lateral leaves (vs. usually with 2 false veins, one at each side of the midrib or at least at one side), lateral leaves usually acute (vs. acuminate), the flagelliform branches occasionally present, ending in an ill-differentiated, elongate, and rather flattened propagule with dentate leaves (vs. flagelliform branches frequently ending in a well differentiated, round, and globose propagule or bud with ciliate leaves in S. porphyrospora). In addition, S. bernoullii differs from S. porphyrospora by its cream (vs. orange) megaspores, without or with an ill-differentiated (vs. with a well differentiated) equatorial flange, and orange (vs. reddish) microspores (see Fig. 7).

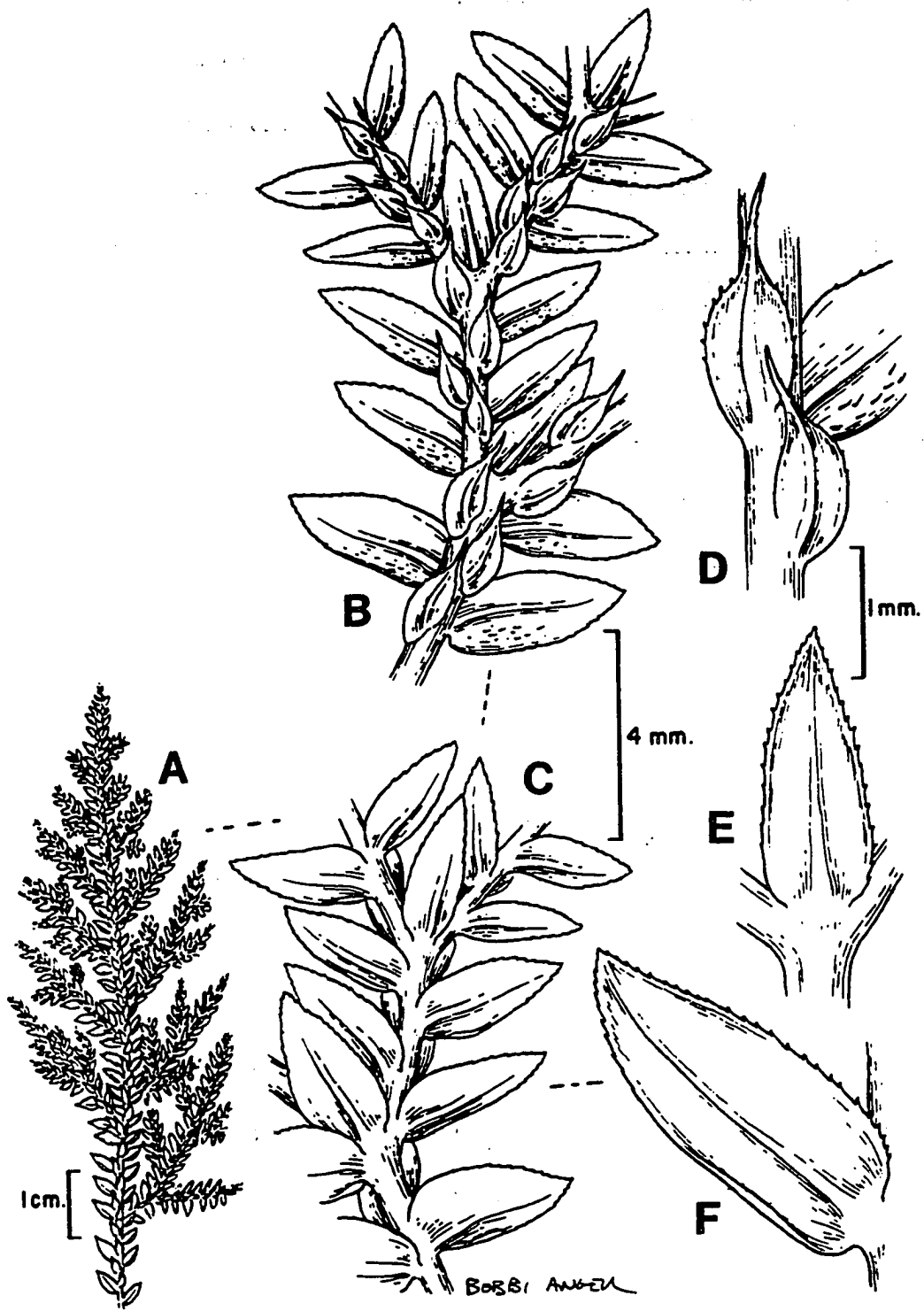
Selaginella bernoullii, in addition to reproducing sexually, propagates vegetatively by sending out stolons which form a tuber-like bud at the tip. These buds are reddish (fide Moran 5548, NY), rather elongate, stout, and covered with hyaline, scale-like leaves. Upon germination they develop a suberect, aerial, branched stem. This new plant in turn can produce new stolons, repeating the cycle. Theoretically, a population of this species may be a clone of a single plant.

Selaginella bernoullii is also characterized by the asymmetric halves of both

lateral and axillary leaves. In both cases one half (the acroscopic one in lateral leaves) is at least  $\frac{1}{4}$  to  $\frac{1}{2}$  wider than the other half.

A specimen at US of Purpus 6720 is S. bernoullii, whereas duplicates of the same collection number at BM, M, NY and UC represent S. porphyrospora. Presumably, both species were growing together and were collected as part of a single gathering, which suggests that they are sympatric.

Fig. 14. A-F. Selaginella bernoullii (Mickel 5092, NY). A. Habit. B. Upper surface of branch. C. Lower surface of branch. D. Median leaves. E. Axillary leaf. F. Lateral leaf.



**19. *Selaginella porphyrospora* A. Braun, Ann. Sci. Nat. Bot. V, 3: 286. 1865. (Figs. 7A-E; 15A-G).**

Type. MEXICO. VERACRUZ: [Mirador?], 3000-6000 ft [915-1830 m], 1856, Sartorius (Holotype: B!, fragment BM!).

*Selaginella bulbifera* Baker, Gard. Chron. 1867: 783, 950. 1867.

Type: from garden material of unknown origin (fide Alston et al. p. 214. 1981).

*Selaginella binervis* Liebmann ex Baker, J. Bot. 22: 112. 1884.

Type: MEXICO. VERACRUZ: Dos Puentes, San Antonio Huatusco, Liebmann (Holotype: K!; isotypes: B-n.v., C-n.v., P-n.v. [fide Alston, 1952: 250; Mickel & Beitel, 1988: 348.], fragment US!).

*Selaginella binervis* Liebmann ex Fournier, Mexic. Pl. 1: 148. 1872, nom. nud. pro syn.

Plants terrestrial or epipetric. Stems creeping, ascending to suberect, stramineous or greenish, (3-)5-12(-23) cm long, 0.2-0.5 mm diam., not articulate, frequently with flagelliform branch and stem apices bearing tuber-like buds at the tip, stoloniferous, 1-3-branched. Rhizophores axillary, restricted to basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem, filiform, 0.06-0.3 mm diam. Leaves dimorphic throughout, membranous to chartaceous, the upper surface green, composed of polygonal to  $\pm$  rounded cells with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant,



perpendicular to the stem or ascending, ovate or semicordiform,  $2-3.4 \times 1-2$  mm, base rounded to semicordate, the acroscopic base strongly overlapping the stem, the basiscopic base not overlapping the stem; the acroscopic margin hyaline, serrate or ciliate-denticulate basally to serrulate apically, the basiscopic margin greenish to pale green, entire to sparsely serrulate; especially apically, the basiscopic margin frequently with stomata; apex acuminate, dentate at tip; the upper surface usually puberulent, especially near basiscopic margin, without stomata, both surfaces or either one usually with two or at least one large, elongate idioblasts or hyaline fibers (false veins) along both sides of midrib, or occasionally these false veins absent, the lower surface glabrous, with stomata along midrib. Median leaves distant to slightly imbricate apically, ascending, ovate, ovate-elliptic, or ovate-lanceolate,  $0.9-1.5 \times 0.5-0.85$  mm; base asymmetric, usually with the inner base truncate and the outer base decurrent, or oblique; margins hyaline, sparsely serrate to serrulate; apex abruptly aristate, the arista almost  $\frac{1}{2}$  or more the length of the lamina,  $0.4-0.82$  mm long, obscurely puberulent and dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib, the lower surface without idioblasts and stomata. Axillary leaves similar to lateral leaves. Strobili terminal on branch tips, lax and flattened, dorsiventral, or occasionally weakly quadrangular,  $3-20$  mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{1}{4}$  to  $\frac{3}{4}$  the sporophyll length, or infrequently ill-defined, asymmetric or ovate to ovate-lanceolate,  $1.5-2.2 \times 0.5-1.2$

mm, with a strongly developed, denticulate keel along midrib, the base rounded, the margins hyaline, sparsely serrate to serrulate, the apex short- to long-acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, puberulent, without idioblasts, usually with conspicuous stomata only along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls pale green to hyaline, ascending, pseudopeltately attached to the axis without an adaxial flap, broadly ovate or broadly ovate-elliptic,  $1.4-1.9 \times 0.6-1.0$  mm, with a slightly developed, entire keel along midrib, the base rounded, the margins hyaline, serrate to serrulate, or denticulate-serrate, the apex long-acuminate to short-aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, or the lower surface with some conspicuous idioblasts, the stomata present only on the lower surface. Megasporangia in two ventral rows, absent, or strobili wholly megasporangiate; megaspores orange, with a well developed equatorial flange, the proximal face reticulate to reticulate-rugulate with close reticulum of high, dense ridges, the distal face reticulate with open reticulum of high ridges,  $250-265 \mu\text{m}$  diam. Microsporangia in two dorsal rows, absent, or strobili wholly microsporangiate; microspores not studied.

**HABITAT AND DISTRIBUTION:** On moist banks and wet mossy rocks in or near waterfalls, streams, roadside banks, or forest clearings, mostly in humid

forest; 450-2800 m; Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, and Ecuador.

SPECIMENS EXAMINED: MEXICO. COLIMA: SW foothills of Nevado de Colima, 1-1.5 mi above (S of) Hacienda San Antonio, 1200-1250, 11 Aug 1957, McVaugh 16097A (US). CHIAPAS: Angel Albino Corzo, along Río Cuxtepeques near finca Gadow, 1270 m, 12 Sep 1976, Breedlove 40118 (DS), 40124 (DS p.p., ENCB); Ixtapa, near Ixtapa, 915 m, 21 Jul 1981, Breedlove 51651 (CAS); La Trinitaria, near Colonia Carmen Xhan and the ruins of Chinkultik, 1525 m, 9 Aug 1981, Breedlove 52025 (CAS); [Motozintla de Mendoza?], Cerro de Boquerón, Sep 1913, Purpus 6720 (BM, F, GH, M, NY, UC); Motozintla de Mendoza, 45-50 km NE of Huixtla along road to Motozintla, 1900 m, 18 Sep 1976, Breedlove 40220 (DS); Santa Magdalena, 1904, G. Münch 136 (DS); Unión Juárez, SW slope of Volcán Tacaná above Talquian, 2200 m, 13 Nov 1976, Breedlove 42548 (DS); Unión Juárez, SE side of Volcán Tacaná above Talquian, 2200 m, 23 Nov 1980, Breedlove & Almeda 47756 (CAS); [Unión Juárez,] Mt. Tacaná, 1000-2000 m, Aug 1938, Matuda 2468 (MICH); Unión Juárez, ladera SW del Volcán Tacaná, 4 km de Talquián rumbo al Chiquihuite, 1480 m, 18 Oct 1985, Riba et al. 1400 (ENCB). GUERRERO: ca. 10 mi N of Taxco, 6 Sep 1959, O. Degener & I. Degener 26278 (BM, NY, US, W). HIDALGO: Trinidad Iron Works, 5500 ft [1677], 2 Aug 1904, Pringle 13260 (CAS, GH, K, L, M, P, US); Zacualtipan, Zacualtipan on road to Soyatla, 1980 m, 28 Oct 1983, Breedlove & Almeda 59427 (CAS, NY). JALISCO:

Amena, El Agostadero, 1500 m, 26 Oct 1985, Sada 16163 (UC); Cerro de La Capilla, camino Talpa-Mascota, 1500 m, 25 Oct 1985, Ruelas 16179 (UC); near Guadalajara, 7 Dec 1888, Pringle 2039 (NY), Sep 1889, Pringle 2593 (BM, BR, DS, F, K, NY-2 sheets, P, UC, US, W); above (N of) La Cuesta, road to the pass crossing to Talpa de Allende, 800-1400 m, 15-16 Oct 1960, McVaugh 20278 (CAS, NY); La Manzanilla, 2200 m, 18 Aug 1985, A. Ortíz 16972 (UC); Los Volcanes, 1900 m, 30 Oct 1973, Breedlove 35840 (CAS, MO); ½ km S of Puento San Pedro, on road from Colima to Ciudad Guzman, 19°20'N, 103°23'W, 1700 m, 31 Jul 1960, Iltis et al. 622 (GH); Río Blanco, Jun-Oct 1886, E. Palmer 558 (BM, GH, K, NY-2 sheets, US); near Santa Mónica, 1950-2050 m, 12-13 Nov 1952, McVaugh 14072 (US); Sierra de Manatlán (15-20 mi SE of Autlán) S and W of the divide between Aserradero San Miguel Uno and Durazno, ca 1700 m, 7 Nov 1952, McVaugh 13967 (US), 14012 (BM, US); Volcán de Tequila, 6-10 km SW of Tequila, 1800-2100 m, 8 Nov 1974, Breedlove 39328 (CAS). México: El Oro, Nov 1910, Rangel in Arsène 10683 (US). MICHOACÁN: Hwy 120 from La Huacana to Ario de Rosales, 13.7 mi N of Ario de Rosales and 1 mi N of San Joaquin turnoff, 19°07'N, 101°43'W, 1500 m, 23 Sep 1986, Yatskievych & Gastony 86-304 (MO); Morelia, Cerro Azul, 2200 m, 1910, Arsène 47 (US, W); Morelia, Cerro Azul, 2200, 1910, Arsène 362 (P); Cerro Azul, 2200 m, 1910, Arsène 5182 (BM); Cerro San Miguel, vicinity of Morelia, 2100 m, 15 Sep 1910, Arsène 6648 (US); Queréndaro, 2 km N de Real de Otzumatlán, 2350 m, 20 Nov 1986, Rzedowskii 41829 (MEXU p.p.); ca. 1 mi SW of Nuevo San Juan Parangicutiro on road from

Uruapán, 19°24'N, 102°09'W, ca. 2000 m, 23 Sep 1986, Yatskievych & Gastony 86-293 (MO); E of San Juan Nuevo (ca. 8 km S of Uruapán), ca. 6100 ft [1860 m], 11-15 Oct 1961, King & Soderstrom 4746 (NY, UC, US); Sierra del Tigre, 3 mi S of Mazamitla, 2100-2200 m, 17 Sep 1952, McVaugh 12995 (BM); Tzararacua, 26 Oct 1985, Alba 17097 (UC). MORELOS: Near Cuernavaca, 13 Nov 1902, Pringle (P); El Parge, 1 Sep 1910, Orcutt 4401 (DS); barranca San Antonio, 10 Sep 1903, Rose & Painter 6943 (BM, US); 21 Sep 1903, Rose & Painter 7250 (BM). OAXACA: Ixtlán, 2 km E of Natividad, from San Pedro Nolasco to the Llano Verde, 6000-6800 ft [1830-2074 m], 4 Oct 1969, Mickel 3748 (NY-2 sheets, UC); Juquila, 88 km S of Sola de Vega, 33 km S of bridge at Juchatengo, 41 km N of San Gabriel, 6050 ft [1845 m], 9 Aug 1971, Mickel 6016 (NY, UC); Mixes, vicinity of Zacatepec, along trail N of city for ca. 1 mi, 4700 ft [1433 m], 30 Jul 1964, Mickel 1571, 1574 (NY); Mixes, NW slope of Cerro Zempoaltépetl, trail from Yacoche to Totontepec, 6500-8000 ft [1982-2440 m], 19 Sep 1970, Mickel 4711 (NY, UC); Mixes, E slope of Cerro Zempoaltepetl, 2-3 hrs SW of Zacatepec on trail to Tamazulapam, 5200-6500 ft [1586-1982 m], 22 Sep 1970, Mickel 4872 (NY, UC); Pochutla, 181 km S of Oaxaca, 64 km N of Pochutla, 4500 ft [1372 m], 29 Sep 1970, Mickel 5079 (NY, UC); Putla, 3 km N of Putla, 2500 ft [762 m], 11 Oct 1969, Mickel 3984 (NY), Hellwig 3986 (NY-2 sheets, UC), 8 km N of Putla, 2900 ft [884 m], 11 Oct 1969, Mickel 3996 (NY p.p.), 9-12 km N of Putla, 3000-3300 ft [915-1006 m], 11 Oct 1969, Mickel 4010 (NY, UC), 15 km S of Putla, 12 km N of Mezones, 3000 ft [915 m], 1 Oct 1972, Mickel 6957 (NY). PUEBLA: Apulco, 11 Jan

1970, W. Boege 1334 (CAS); Tezuitlán, 7 Sep 1910, Orcutt 4035 (BM, DS, GH, K, MEXU). SINALOA: 30 km E of La Concordia along road to Durango near El Coco, 1000 m, 27 Oct 1973, Breedlove 35686 (CAS, MICH, MO); Concordia, El Palmito, 2000 m, 23 Sep 1988, Vega 3058 (ENCB); Mazatlán, 1927, Reiche (M). SONORA: Tepopa, Sierra Saguaribo, 3000-3500 ft [915-1067 m], 16-18 Oct 1961, Gentry et al. 19317 (NY, US). VERACRUZ: Coscomatepec, Monument at The Virgin of Guadalupe at crossing of Río de Jamapa on Fortin-Huatusco road, 16°16'N, 96°00'W, 1300 m, 7 Aug 1976, Faden et al. 76/177 (UC); Barranca de Jamapa, cerca de Coscomatepec, 2 Nov 1948, Ruíz (MEXU p.p.); El Durazno, bridge over the Jamapa River, near Chocamán, 27 Aug 1967, Riba et al. 398 (GH); Miahuatlán, Miahuatlán, 19°43'N, 96°51'W, 1750 m, 17 Jun 1979, A. Rodríguez 80 (XAL); Orizaba, 1855, Müller 39bis (NY p.p.); Orizaba, Schaffner 118 (fragment NY, P); Puente sobre el Río Chocamán, 5 km S de Coscomatepec, 1350 m, 11 Oct 1964, Rzedowski 19073 (NY); Zacuapan, Jan 1914, Purpus 7438 (GH, NY, UC, US). WITHOUT SPECIFIC STATE OR LOCALITY: Schmitz 872 (W).

GUATEMALA. ALTA VERAPAZ: Cobán, 1350 m, 15 Nov 1920, H. Johnson 981 (F, S); Cobán [Copán?], 1350 m, Aug 1906, von Türckheim II 1369 (US); Copán, 1400 m, Dec 1907, von Türckheim II 2036 (BM). BAJA VERAPAZ: Sierra de las Minas, 3 km SE of Purulhá, 1800 m, 2 Jan 1974, L. O. Williams et al. 43139a (F), 2000 m, 6 Jan 1974, L. O. Williams et al. 43393 (GH). CHIMALTENANGO: Plains near Tecpán, 2100 m, 29 Sep 1933, Skutch 627 (US); Region of Las Calderas, 1800-2100 m, 22 Nov 1938, Standley 57808 (F); Sierra Madre Mountains,

Cerro Chichoy, ca 10 km NW of Tecpán, 2200-2300 m, 25 Dec 1972, L. O. Williams et al. 41781 (F, GH, NY). **CHIQUMULA:** Socorro Mountains, between Finca San José (1½ mi SE of Concepción de la Minas), and Montaña Nube (Montaña Volcancitos), 1200-1700 m, 1 Nov 1939, Steyermark 30980 (F). **GUATEMALA:** slopes of Volcán de Pacaya, between San Francisco Sales and the base of the active cone, 1800-2300 m, 20 Dec 1940, Standley 80619 (US), 80672 (F). **HUEHUETENANGO:** above San Juan Ixcay, Sierra de los Cuchumatanes, 2400 m, 4 Aug 1942, Steyermark 50006 (F, GH, US). **JALAPA:** NE of Jalapa, 1400-1600 m, 10 Nov 1940, Standley 76811 (F, US), 76862 (US). **QUETZALTENANGO:** 1.7 mi S of bridge at Almolonga along road #9S, 6400 ft [1952 m], 17 Jun 1972, Hellwig & Whitaker 1374, 1375 (NY); vicinity of Fuentes Georginas, slopes of Volcán de Zunil, 2300-2500 m, 3 Feb 1941, Standley 85940 (F); along road 95, ca. 10 mi S of Quetzaltenango, 22 Jun 1972, McAlpin 1072 (CAS); NW slope of Volcán Zunil, 6-8 km of Zunil along road to Fuentes Georginas, 2375 m, 2 Oct 1986, Breedlove & Almeda 64821 (CAS); western slope of Volcán Zunil, opposite Santa María de Jesús, 1500 m, 21 Jan 1940, Steyermark 35160 (US). **QUICHÉ:** Inter Chiché [Quiché] and Chichicastenango, Sep 1870, Bernoulli & Cario 159 (P); El Quiché, above Nebaj, 7200 ft [2196 m], 7 Feb 1945, Sharp 45111 (US). **SOLOLA:** Along road E of Los Encuentros, 2400-2850 m, 11 Jan 1939, Standley 62352 (F). **SACATEPÉQUEZ:** Near Las Lajas, ca. 1200 m, 28 Nov 1938, Standley 58127 (F). **SUCHITEPEQUEZ:** Finca Mora, along shore of lake, 3000 ft [915 m], 4 May 1937, Muenschner 12170 (BM, GH, UC, US). **TOTONICAPÁN:** Sierra Madre Mountains,

near Polagua, 20-25 km N of Cristóbal, 2800 m, 5 Dec 1962, L. O. Williams et al. 22662 (F, G, NY, US, W). ZACAPA: Río Sitio Nuevo, between Santa Rosalía and first waterfall, 1200-1500 m, 9 Jan 1942, Steyermark 42203 (US); Sierra de las Minas, Río Lima, below Finca Alejandria, 2000 m, 14 Oct 1939, Steyermark 30024 (F). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Salamá trail, above Llano Grande, 22 Jan 1905, Maxon & Hay 3413 (F, NY, US); Santa María de Jesús, 13 Sep 1940, Haupt? 104 (US).

HONDURAS. COMAYAGUA: Barranco El Socorro, mountains ca 8 km W of Siguatepeque, 1500 m, 29 Sep-5 Oct 1951, L. O. Williams & R. Williams 18381 (US); Barranco Trincheras, 3 km a Montañuela, 1200 m, 28 Mar 1964, Molina 13660 (F, NY); Cordillera Montecillos, El Cedral, 16 km SW of Siguatepeque, 1400 m, 10 Jan 1969, Molina 23313 (G, NY); vicinity of Siguatepeque, ca. 1050 m, 25 Mar-5 Apr 1947, Standley & Chacón 6285 (US); vicinity of Siguatepeque, 1080-1400 m, 14-27 Feb 1928, Standley 56217 (BM, US). EL PARAÍSO: Güinope, 1430 m, Dec 1943, J. Valerio 1876 (F, US). FRANCISCO MORAZÁN: Mateo, Monte Upare, 1776 m, 15 Oct 1983, Silva 138 (MO); eastern slopes of Peña Blanca, San Juacinto Mountains, 1900-2000 m, 22 Mar 1951, Morton 7307 (BM, BR, CAS, F, G, GH, M, NY, S, U, UC); Quebrada Quemada, km 21 vicinity of Cerro de Hule, 1300 m, 26 Feb 1970, Molina 25405 (BM, GH, NY, S, U); Río Rancho Quemado, SE of Tegucigalpa, kms 20-25 road to Sabana Grande, 1300 m, 9 Nov 1966, Molina 18647 (DS, F, G, GH, NY, U-2 sheets, US, W); mountains above el Jicarito, road to Tatumbula base of Cerro de Uyuca, 1500 m, 30 Oct 1951, Standley



29121 (F, US); Río Yeguaré, caminos Tatumbla, Labranza, y Quebrada El Granadillo, sobre Mt. Uyuca, 14°N, 87°W, 1800 m, 21 Dec 1948, Molina 1429 (US); Río Yeguaré, Mt. de Uyuca, entre Labranza y Quebrada El Granadillo, 14°N, 87°W, 1800 m, 21 Dec 1948, Molina 1864 (F, US); Río Yeguaré, Mt. Uyuca, ca. 14°N, 87°W, 2000 m, 2 Jan 1949, L. O. Williams & Molina 14940 (BM, F, US); Cerro Uyuca, N of Zamorano, toward Tegucigalpa, 1800 m, Hawkes et al. 2021 (F, G, K, S); Cerro de Uyuca, along trail from Las Flores to La Labranza, 1600-1750 m, Oct-Dec 1948, Standley 13402 (F), Standley 14042 (BM, NY), 15652 (BR, CAS, US); lower slopes of Cerro Uyuca, 1530-1600 m, 22 Feb 1947, Standley & Molina 4256 (F); N slope of Montaña Uyuca, near the beginning of the Tatumbla road, 5-7 km E of Tatumbla, 1500 m, 15 Dec 1973, L. O. Williams et al. 42836 (MICH). INTIBUCÁ: Vicinity of La Esperanza, 1500-1600 m, 31 Jan-12 Feb 1950, Standley 25563 (F). LEMPIRA: Celaque National Park, along Río Arcágual, 7.5 km WSW of Gracias, 14°34'N, 88°39'W, 1400 m, 11 Nov 1991, Moran 5522 (NY). OCOTEPEQUE: Cordillera Meredón, El Moral, 1600 m, 27 Aug 1968, Molina 22292 (F, NY).

EL SALVADOR. WITHOUT SPECIFIC PROVINCE OR LOCALITY: Volcán Boquerón, 1750 m, 24 Oct 1952, Lötschert 28 (US); Bosque Montecristo, 1900 m, 2 Feb 1979, Seiler 877 (F, GH, NY); Cerro Los Naranjos, 1550 m, 5 Oct 1978, Seiler 609 (F, NY); San Vicente, 1700 m, 10 Jul 1953, Lötschert 437 (US).

NICARAGUA. GRANADA: summit of Mt. Mombacho, near Granada, 1600 m, 24 Dec 1940, V. Grant 857 (GH); Mombacho Volcano, 1050 m, 5 Jul 1923,

Maxon et al. 7797 (US), 1300 m, 5 Jan 1967, L. O. Williams & Molina 20016 (F, NY, US), 20040 (BM, NY, W); W slope of Volcán Mombacho, above Finca Santa Ana, Plan del Flores, 11°49-50'N, 85°58'W, 950-1150 m, 1 Oct 1977, Stevens 4362 (NY, UC). JINOTEGA: Macizos de Peñas Blancas, between finca of Manuel Estrada (El Cielo) and finca of Socorro Mejia, 13°15-16'N, 85°41'W, 1500-1650 m, 14-18 Jan 1979, Stevens 11706 (UC), 11709 (UC). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Wright 3 (GH, US).

COSTA RICA. ALAJUELA: Hacienda of Ramón González, 1875, Polakowsky 115 (BM, W); Aguas Zarcas, Hacienda La Marina, Río San Rafael, 450-500 m, 8 Feb 1965, L. O. Williams et al. 29055 (F, GH, NY); waterfall La Paz, 18 Feb 1955, Scamman 7540 (GH); catarata La Paz, between Vara Blanca and Cariblanco, 15 Jan 1991, J. Grant et al. 91-1408 (US); Alto de La Calera de San Ramón, 5 Dec 1927, Brenes 5884 (F, NY); vicinity of Fraijanes, 1500-1700 m, 13 Dec 1926, Standley & R. Torres 47704 (BM); La Granja, 12 Mar 1951, Scamman 5839 (GH); La Palma de San Ramón, Sep 1925, Brenes 4468 (F, NY), 24 Nov 1926, Brenes 5118 (NY), 5 Oct 1927, Brenes 5732 (NY); Monteverde Forest Reserve, 10°15'N, 84°50'W, 1400 m, 2 Nov 1986, Hennipman et al. 6642 (UC); Río Jesus, Santiago de San Ramón, 1 Jan 1937, Brenes 21857 (F, NY), 21886 (NY); Río San Rafael, 2 km W of La Marina, Llanuras de San Carlos, 550 m, 17 Feb 1966, Molina et al. 17376 (F, NY, US, W); San Pedro de San Ramón, 5 Jan 1937, Brenes 21875 (NY); San Ramón, Reserva Forestal San Lorenzo, 900-1000 m, 16 Apr 1982, Carvajal 128 (MO); 1-3 km E of San Ramón, 10°05'N, 84°27'W, ca. 1000 m, 13-14

Apr 1983, Liesner 14210 (MO, UC); along road from Vara Blanca (between Poás and Barva volcanoes) to La Concordia, 1600-1950 m, 23 Jul 1923, Maxon & Harvey 8485 (US); Vara Blanca de Sarapiquí, N slope of Central Cordillera, 1500-1750 m, Jul-Sep 1937, Skutch 3190 (BM, GH, K, NY, S, US), between Poás and Barva volcanoes, 1800 m, Oct 1937, Skutch 3375 (GH, K, NY), 1400 m, Feb 1938, Skutch 3491 (K, NY, S, US); slopes of Volcán Poás at bridge just below Hacienda El Tirol, 2000 m, 6 Jul 1967, Mickel 2451 (NY); near Zapote on the road to Villa Quesada, 4000-4500 ft [1220-1372 m], 24-27 Mar 1955, Scamman 7543 (GH).

**ALAJUELA-HEREDIA:** Border between Alajuela and Heredia, above Vara Blanca, 9 Jul 1972, McAlpin 1285 (CAS, F). **CARTAGO:** Dulce Nombre, 1400 m, 27 Feb 1924, Standley 35950 (US); El Muñeco, S of Navarro, 1400 m, 8-9 Feb 1924, Standley 33684 (US); W slope of Irazú, 1500 m, 27 Dec 1881, Lehmann 1032 (BM, US); Navarro, s.d., Lankester (BM, US); Orosi, 5000 ft [1525 m], 24, 31 Mar 1951, Scamman 5841 (GH); near the bridge over the Río Tiribí on the road Ipís to Tierra Blanca, 1600-1700 m, 4 Jul 1970, Lellinger & White 935 (UC, US); ca. 10 km S of Tapantí along the new road on the E slope above Río Grande de Orosi, 9°42'N, 83°47'W, 1400-1600 m, 10-24 Jun 1968, Burger & Liesner 5674-A (GH); ca. 15 km S of Tapantí along the new road, on the E slope above the Río Grande de Orosi near the concrete bridge, 9°42'N, 83°47'W, 1500 m, 12, 14, 17 Dec 1969, Burger & Liesner 6815 (F, GH); new road from Tapantí, ca. 7 km S of bridge, 1500 m, 13 May 1967, Hauke 419 (NY); 17 km SE of Tapantí, 1700 m, 27 Apr 1969, Lent 1642 (F); along trail leading eastward into mountains from road

into Tapanti Reserve (also known as "Quebrada Val Verde"), ca. 1 km S of jct. of Quebrada Salto and Río Grande de Orosi, 9°43'N, 83°47'W, 1500-1800 m, 1 Feb 1986, A. R. Smith et al. 2145 (UC); Mountains above Tres Ríos, ca. 5000 ft [1525 m], 17 Mar 1956, Scamman & Holdridge 7819 (GH); NE of Turrialba, just W of Santa Cruz near side road to Volcán Irazú, ca. 1600 m, 5 Aug 1970, Lellinger & White 1461 (US). **HEREDIA:** Cinchona, above the Upper Sarapiquí Valley, 4000 ft [1220 m], 20 Mar 1955, Scamman 7542 (GH, US p.p.); Finca Montecristo, off rt. 113, 1800 m, 28 Jul 1983, Moran 3322 (MO, UC); Heredia, 23 Dec 1934, Brenes [7] (NY); La Palma, Finca Miravalles, 1500 m, Horich [Acc. No. 58.595-1] (GH, K, MICH, UC); Palma, 1400 m, 2 Dec 1908, Brade 284 (NY, UC); La Palma, 1500 m, 31 Jul 1936, M. Valerio 2243 (US); Yerba Buena, NE of San Isidro, 2000 m, 22, 28 Feb 1926, Standley & J. Valerio 49696 (US); faldas del Volcán Barva, 1800 m, 26 Jun 1926, M. Valerio 1 (US). **PUNTARENAS:** Monteverde Forest Reserve, 1600 m, 12 Jun 1975, Lellinger et al. 1746 (NY); foothills of the Cordillera de Talamanca, Sitio Coto Brus, ca. 8°59'N, 82°46'W, 1800-1900 m, 3 Sep 1983, Davidse 24524 (UC). **SAN JOSÉ:** Between Acerri and Tarbaco, ca. 18 km from San José, 5750 ft [1754 m], 2 Aug 1961, C. Brown CR-233 (US); Cerro Chirripó, lower SW slopes, along trail from Canaan to summit, 5500-7000 ft [1677-2135 m], 21, 27 Aug 1967, Evans et al. 6 (U, US); NE of Coronado, ca. 10 mi NE of San José, ca. 1500 m, 31 Jul 1940, Chrysler & Roever 5326 (US); Desamparados, Sep 1889, Tonduz 924a (P), 14 Sep 1889, Tonduz 927 (BR, US); vicinity of El General, 1190 m, Dec 1935, Skutch 2332 (GH, K, NY, S, US);

vicinity of La Hondura (4 km S to 1 km N on Rte 220) between Volcán Irazú and Volcán Barva, 1250-1500 m, 25 Mar 1967, Mickel 2231, 2269 (NY); La Hondura, 1200-1500 m, 9 Mar 1926, Standley & J. Valerio 51865 (BM, F); between La Palma and La Hondura (1-4 km S of La Hondura) on Rte 220, between Volcán Irazú and Volcán Barva, 1500 m, 9 Jul 1967, Mickel 2520 (NY); above La Hondura Valley, La Palma area ca. 9 km NE of San Jerónimo, 10°02'N, 84°00'W, ca. 1500 m, 23 Mar 1973, Stolze 1440 (F, US); Las Nubes, 5000 ft [1525 m], 18 Feb 1956, Scamman & Holdridge 7818 (GH), 1500-1900 m, 20-22 Mar 1924, Standley 38358 (US), 1800 m, 28 Jul 1936, M. Valerio 2238 (US); La Palma on the road to La Hondura, 4700-4800 ft [1433-1464 m], 5-6 Mar 1955, Scamman 7541 (GH); old road to Limón, 7.4 km N of San Jerónimo at La Palma, 10°10'N, 84°00'W, 1400-1500 m, 13 Jan 1987, Hill et al. 17761 (NY); Pérez Zeledón, near Canaan, 1300 m, 7 Dec 1966, Hauke & López 349 (NY); Río Claro valley, below La Palma NE of San Jerónimo, 10°03'N, 83°58'W, 1000-1200 m, 19 Nov 1969, Burger & Liesner 6267 (F, NY, US); Río Lajas, ca. 6.4 km E of Santo Domingo, Dec 1974, J. Taylor 17436 (NY); Río Zurquí, Cordillera Central, 10°4'N, 84°1'W, 1500-1600 m, 18 Jan 1986, A. R. Smith et al. 1656, 1735 (UC); above San Isidro del General (Urena), 6000 ft [1830 m], 7 Nov 1961, Rosbach 3229 (GH); vicinity of Tarbaca (1 km S and 2 km N), 1600-1750 m, 5 Jul 1967, Mickel 2391 (NY).

WITHOUT SPECIFIC PROVINCE OR LOCALITY: Endres 409 (W); Candelaria, 1500 m, 4 Aug 1908, Brade 830 (S), 17 Dec 1909, Brade 836 (NY, S p.p., UC); Frazn, 2000 m, 8 Sep 1908, Brade 71 (K, UC, US), [Brade?] 239 (S); La Uruca, Jul 1888,

Biolley 927 (P); Río Virilla, Oct 1898, Tonduz 12715 (P); Zapote de San Carlos, 16 May 1938, A. Smith PC 314 (F).

PANAMA. CHIRIQUÍ: 4 km SW of Las Mellizas in Costa Rica, just across the border into Panama, 26 Dec 1992, J. Grant & Rundell 92-2242 (NY, US); Boquete, Valley of Río Piarnasta, 1550-1650 m, 22 Jul 1918, E. P. Killip 5402 (US); 11 km NW of Río Chiriquí Viejo bridge towards Río Serrano, ca. 2000 m, 17 Mar 1977, D'Arcy 10750 (MO); Fortuna Dam area, N fork of Quebrada Arena, 8°46'N, 82°12'W, 1100 m, 6 Feb 1984, H. Churchill et al. 4677 (MO); along trail between N fork of Río Palo Alto and Cerro Pate Macho, ca. 6 km NE of Boquete, 8°48'N, 82°23.5'W, 1600-2000 m, 6 Feb 1986, A. R. Smith et al. 2365 (UC), 2403 (MO, NY, UC).

COLOMBIA. ANTIOQUIA: [San Agustín?], Oct [1888?], Kalbreyer [187] (S); Yarumal, carretera a la Costa, entre Yarumal y Ventanas, 2030 m, 5 May 1983, Santa 604 (COL). BOYACÁ: Trail from Bocota to Bachira, N bank of the Río Royata, 2050 m, 25 Aug 1957, Grubb & Guymer P.95 (BM, COL, US); Carretera Sogamoso-Pajarito, finca Comijoque, orilla del Río Cusiana, 1800 m, 11 Oct 1967, Hagemann 664 (COL). CUNDINAMARCA: Carretera Gutiérrez a Une, ca. 2700 m, 12 Oct 1974, Acosta-Arteaga 804 (COL); Cordillera Oriental, Cerinza, Río Blanco Valley, 7 km E of Gutiérrez, 50 km S of Bogotá, 1875 m, 29 Jul 1944, M. Grant 9756 (COL). META: Uribe, Río Duda, 770 m, 21 Dec 1942, Fosberg 19469 (GH); W of Villavicencio, 700-800 m, 15 Oct 1972, Hagemann & Leist 1196 (COL), 1199 (COL). NORTE DE SANTANDER: Cordillera Oriental, región de Sarare, Hoya del

Río Chitagá, sobre La Cabuya, 1600-1800 m, 13 Oct 1941, Cuatrecasas et al. 12187 (COL, GH).

VENEZUELA. **BARINAS:** Barinitas, St. Domingo, ca. 1250 m, 28 Sep 1968, B. Oberwinkler & F. Oberwinkler 12851 (M); Bolívar, near Feldspar mine, between Altamira and Santo Domingo, 8°51'N, 71°35'W, 1300 m, 5 Aug 1983, van der Werff & R. Ortíz 5901 (MO- 2 sheets, UC). **BOLÍVAR:** Sierra de Lema, headwaters of Río Chicanán, 80 km SE of El Dorado, 6°05'N, 62°W, 500 m, 28 Aug 1961, Steyermark 89599 (NY p.p.); vicinity of Salto de Pacairao bordering Río Pacairao, ca. 3 km E to NE of Santa Teresita de Kavanayén, 1220 m, 24 Nov 1944, Steyermark 60523 (F, MO, NY, S, US). **LARA:** Jiménez, Parque Nacional Yacambú, 3 km E of Park headquarters, Quebrada El Blanco, 9°43'N, 64°34'W, 1300-1400 m, 24 Oct 1982, Davidse & González 21107 (UC), 21114 (MO); Quebrada Cedral, región de El Blanquito, 17 km SSE de Sanare, 1660 m, 6 Aug 1970, Steyermark et al. 103495 (US); Morán [Andrés Eloy Blanco], 8.7 mi SE of Sanare, Parque Yacambú (3.4 mi beyond park entrance), 9°41'N, 69°35'W, ca. 1500 m, A. R. Smith et al. 1243 (MO, UC), 1253 (UC). **MÉRIDA:** Sierra de Mérida, supra Maracaibo, Ernst 87 (S). **WITHOUT SPECIFIC PROVINCE OR LOCALITY:** Encanto, Vogl (M); Río Amana, Helvecia, 1730 m, 26 Jan 1930, Netting 11 (F); Timotes, Vogl (M).

ECUADOR. **CARCHI:** Maldonado, SW of the village, 1500 m, 8 Oct 1981, Werling & Nielssen 388 (QCA). **NAPO:** road from Quito to Baeza, km 150, 1800 m, Jan 1979, Besse et al. 30 (QCA); unión of Río Borja and Río Quijos, W bank,

0°25'S, 77°49'W, 1750 m, 19 Sep 1980, Holm-Nielsen et al. 26171 (AAU).

PASTAZA: 5 km E of Mera, on road to Sheell Mera, 1°28'S, 78°05'W, 1050 m, 30 Jul 1980, Ollgaard et al. 35559 (AAU).

NOMENCLATURAL COMMENTS: The name S. sarmentosa Liebmann ex Fournier, nom. nud. (not A. Braun) apparently belongs here. I have seen a photograph of Liebmann's illustration of it at NY and concluded it is the same as S. porphyrospora.

TAXONOMIC DISCUSSION: Selaginella porphyrospora, as previously noted, is closely related to S. bernoullii, and both form a clade. These two species have been amply discussed above under S. bernoullii. Selaginella popayanensis also has puberulent lateral leaves but can be distinguished from S. porphyrospora by its lack of false veins or conspicuous idioblasts on the upper surface of the lateral leaves, light orange microspores, and acute lateral leaves. The microsporangia of S. porphyrospora, with their microspores contained within, have a distinct raspberry-red color, which, although not purple, may be the source of the species epithet (Mickel & Beitel, 1988).

As has been previously reported (Alston, 1955), some specimens of S. porphyrospora lack conspicuous false veins or/and conspicuous hairs on the upper surface. For the most part these specimens are easily distinguished by the other characteristics here mentioned, and in other cases both hairs and false veins are

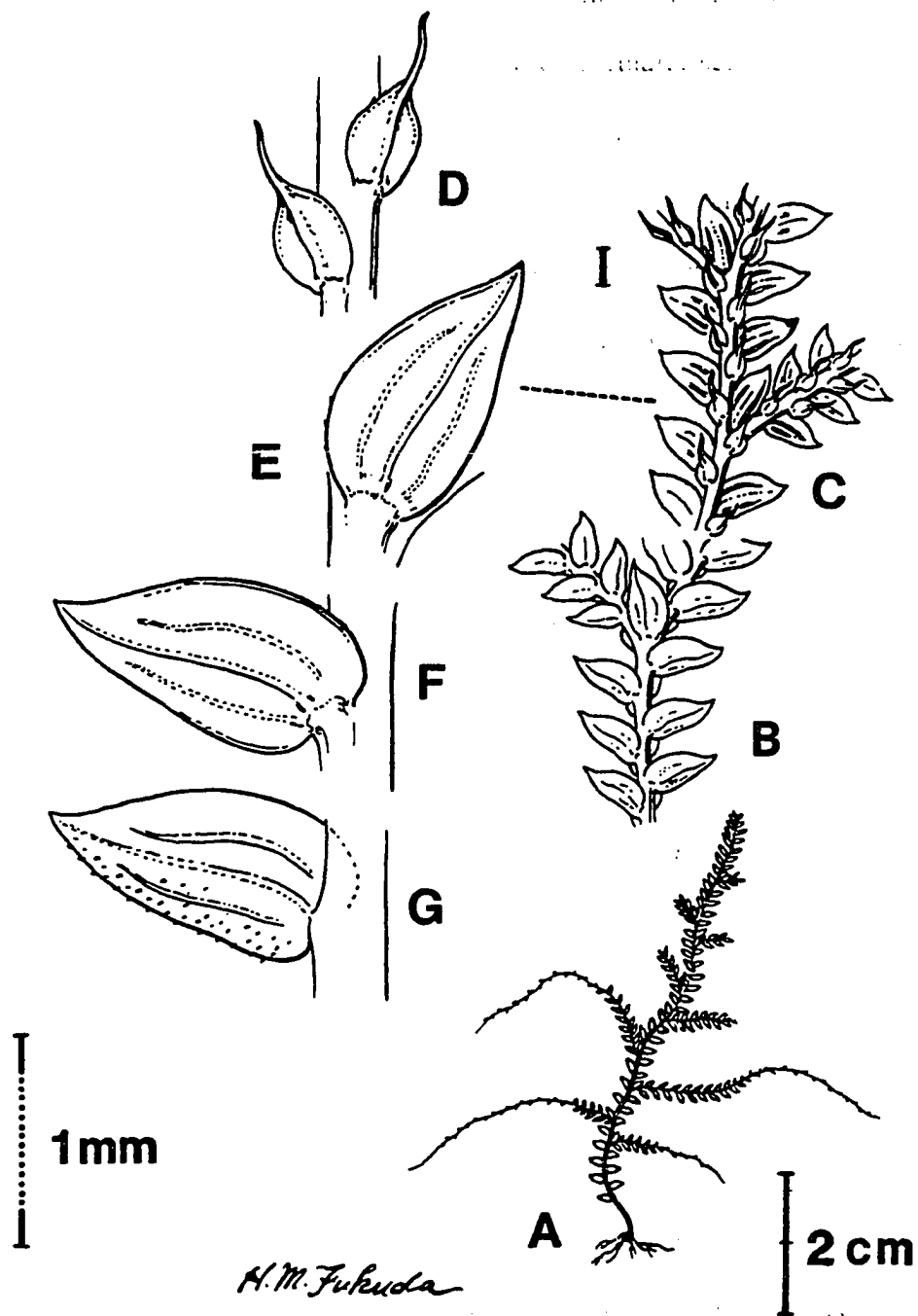


present but are not readily observed. As pointed out by Smith (1981), and in agreement with other neotropical species of subg. Heterostachys here treated, S. porphyrospora is variable in regard to sex expression in the strobili. Some specimens have only megasporangiate or microsporangiate strobili. The exact mechanism by which this phenomenon occurs is still unknown. It is probably an endogenous mechanism by which heterospory is regulated in Selaginella, and at least one study (Brooks, 1973) suggests that it might be influenced by hormones, particularly ethylene.

Selaginella porphyrospora, as mentioned in the description, is also distinguished by flagelliform branch, stem, and strobilus apices, which typically produce round buds at the tip.

Pringle 2593 at BM, DS, F, K, UC, W is S. porphyrospora, but at M, NY, P, and US it is a mixture of S. porphyrospora and S. lineolata. I have numbered them Pringle 2593 and Pringle 2593a, respectively, in order to be consistent with a previously numbered specimen at BR!, Pringle 2593a, which also represents S. lineolata.

Fig. 15. A-G. Selaginella porphyrospora (Mickel 3984, NY). A. Habit. B. Lower surface of branch. C. Upper surface of branch. D. Median leaves. E. Axillary leaf. F. Lateral leaves, lower surface; note elongate idioblasts at both sides of the midrib. G. Lateral leaves, upper surface; note submarginal hairs and elongate idioblasts at both sides of the midrib.



**20. *Selaginella glossophylla* Alston ex Crabbe & Jermy, Fern Gaz. 11: 259. 1976.**

Type: BOLIVIA. COCHABAMBA: [Chapare,] Incachaca, power station ca. 80 mi [129 km] NE of Cochabamba, 17°00'N [S], 65°30'W, 10000 ft [3050 m], 22 Aug 1950, Brooke 6783 (Holotype: BM!; isotype: F!).

Plants probably terrestrial. Stems creeping to ascending, stramineous, 5-8 cm long, 0.32-0.5 mm diam., not articulate, not flagelliform, stoloniferous, 1- or 2-branched. Rhizophores axillary, restricted to basal ½ of the stem, filiform, 0.06-0.16 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to ± rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, broadly oblong or oblong-elliptic, 1.8-2.4 × 1.1-1.3 mm; base rounded, the acroscopic base slightly to strongly overlapping the stem, the basiscopic base not overlapping the stem; margins greenish, entire or serrulate, without conspicuous stomata; apex broadly rounded to obtuse, dentate at tip; the upper surface glabrous, without idioblasts or conspicuous stomata, the lower surface glabrous, with obscure idioblasts, and with stomata along midrib. Median leaves distant, ascending, obovate, 1.2-1.45 × 0.6-0.7 mm; base asymmetric or oblique; the inner margin hyaline, serrate to serrulate, the outer margin greenish, entire along basal ½, serrate to serrulate along apical ½; apex acute, dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib, especially along apical ½ and

submarginal to marginal along the basal  $\frac{1}{2}$  of the outer margin, the lower surface without idioblasts or stomata. Axillary leaves similar to lateral leaves. Strobili terminal on branch tips and stem apex, lax and flattened, dorsiventral, 2-5 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{1}{2}$  to  $\frac{3}{4}$  the sporophyll length, asymmetric, lanceolate, or ovate,  $1.36-1.64 \times 0.6-0.95$  mm, with a well developed, denticulate keel along midrib, the base rounded, the margins narrowly hyaline to pale green, serrulate, the apex acute, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts and usually with obscure stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis, without an adaxial flap, elliptic to elliptic-ovate,  $1.28-1.46 \times 0.58-0.78$  mm, with a very weakly developed, entire to denticulate keel along midrib, the base rounded, the margins hyaline to pale green, serrulate to entire, the apex acute, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present along the midrib. Megasporangia in two ventral rows; megaspores pale to light orange-yellow, without an equatorial flange, the proximal face rugose to rugose-reticulate with close reticulum of rather low ridges, the distal face reticulate with open reticulum of high ridges, 275-290  $\mu$ m diam. Microsporangia in two dorsal rows and

occasionally few in apical region in dorsal rows; microspores not observed [ca. 34  $\mu\text{m}$  diam., according to Crabbe & Jermy, 1976].

**HABITAT AND DISTRIBUTION:** Habitat unknown; 3050 m; known only from Bolivia.

**SPECIMEN EXAMINED:** BOLIVIA. COCHABAMBA: [Chapare,] Incachaca, power station ca. 80 mi [129 km] NE of Cochabamba, 17°00'N [S], 65°30'W, 10000 ft [3050 m], 22 Aug 1950, Brooke 6783 (BM, F, type coll. of S. glossophylla).

**TAXONOMIC DISCUSSION:** Selaginella glossophylla is easily distinguished from other neotropical species of Selaginella, except S. salazariae Valdespino (which is not treated here), by its obovate median leaves and oblong or oblong-elliptic lateral leaves, which have a rounded to obtuse apex. Selaginella glossophylla differs from S. salazariae by lacking (vs. having) conspicuous stomata throughout the upper surface of the median leaves and dorsal sporophylls, the median leaves with an acute (vs. abruptly cuspidate to abruptly short-aristate) apex, and the lateral leaves perpendicular to the stem (vs. ascending).

The isotype at F, has a different elevation, 8000 ft [2440 m], than the holotype at BM, 10000 ft [3050 m].

Crabbe and Jermy (1976) cited a collection supposedly from Chile, according to the label, "1848 Mercier s.n. (P!)," as a paratype of S. glossophylla.

I have examined this collection and believe it to be a different taxon and perhaps a new species. It differs from S. glossophylla by having the median leaves elliptic to elliptic-ovate, frequently with a weakly developed outer auricle, the lateral leaves narrowly oblong with the margins definitively serrate to serrulate, with both halves symmetrical (not asymmetrical as in S. glossophylla), the dorsal sporophylls with conspicuous stomata along midrib and on apical  $\frac{1}{3}$  of the lamina, and ventral sporophylls lanceolate to lance-ovate with the apex gradually attenuate.

A detached and mature megaspore found in the soil present on this collection (Mercier s.n.) has a snow-white color, but examination of an immature megasporangium yielded yellowish, immature megaspores. In both cases, however, megaspores were smooth on the distal face rather than reticulate and orange as in S. glossophylla. I hesitate in describing Mercier s.n. as a new species because the material available at the present time is too scanty and the collection data are rather incomplete and may be misleading.

**21. *Selaginella mixteca* Mickel & Beitel, Mem. New York Bot. Gard. 46: 345.**

1988. (Figs. 16A-G).

Type. MEXICO. OAXACA: Sola de Vega, 23-29 km S of Sola de Vega, 27-33 km N of bridge at Juchatengo, 5200-6200 ft [1586-1891 m], 11 Aug 1971, Mickel 6321 (Holotype: NY!; isotype: UC!).

Plants terrestrial or epipetric. Stems suberect to erect, stramineous, 4.5-13 cm long, 0.35-0.8 mm diam., not articulate, not flagelliform, stoloniferous, 2- or 3-branched. Rhizophores axillary-ventral or ventral, restricted to lower most base, mostly on underground stolons, filiform, 0.16-0.28 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded to cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, broadly ovate, ovate-lanceolate, or ovate-oblong, 2.3-3  $\times$  1.3-1.7 mm; the acroscopic base rounded, strongly overlapping the stem, the basiscopic base truncate to geniculate, not overlapping the stem; the acroscopic margin greenish to pale green, long-ciliate along basal  $\frac{1}{2}$  to  $\frac{1}{3}$ , otherwise entire to serrulate apically, the basiscopic margin pale green, serrulate or entire throughout, the basiscopic margin without conspicuous stomata; apex broadly acute to acute, dentate at tip or ciliolate on leaves along basal part of stem; the upper surface glabrous, without idioblasts or stomata, the lower surface glabrous, usually without conspicuous idioblasts, with stomata along midrib. Median leaves distant,



ascending, broadly ovate to ovate-lanceolate,  $1.2-1.94 \times 0.7-0.96$  mm; base asymmetric, rounded, or subcordate; margins hyaline, long-ciliate on leaves along basal part of the stem, short-ciliate to ciliate-denticulate, serrate to serrulate, or the inner margin shortly ciliate and the outer margin serrate on leaves generally above first branch; apex acute and ending in cilia on leaves along basal part of the stem, or gradually long-acuminate to long-aristate on leaves above first branch, the acumen or arista  $\frac{1}{2}$  or less the length of the lamina, 0.06-0.5 mm long, dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib, the lower surface without idioblasts or stomata. Axillary leaves similar to lateral leaves or more oblong. Strobili terminal on branch tips and stem apex, slightly lax and flattened, dorsiventral, 2-4 mm long. Sporophylls weakly dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a weakly developed adaxial flap extending along  $\frac{1}{4}$  to  $\frac{1}{2}$  the sporophyll length, asymmetric or ovate,  $0.86-1.42 \times 0.52-0.7$  m, with a slightly developed, denticulate keel along midrib, the base rounded, the margins hyaline, serrate, the apex shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts, with or without obscure stomata throughout, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts or stomata; ventral sporophylls pale green, ascending, basally to pseudopeltately attached to the axis, without an adaxial flap, ovate,  $1.34-1.56 \times 0.8-1.02$  mm, with a slightly developed,

denticulate to entire keel along midrib, the base rounded, the margins hyaline, ciliate-denticulate along basal  $\frac{2}{3}$ , serrate to serrulate apically, the apex acute, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present only on the lower surface. Megasporangia only a single one at the base of the ventral sporophylls; megaspores pinard to baryta yellow (lemon-yellow), with or without an equatorial flange, the proximal face seemingly striate-reticulate with close reticulum of low ridges, the distal face reticulate with close to open reticulum of low ridges, 320-360  $\mu\text{m}$  diam. Microsporangia almost occupying the entire strobili; microspores not studied.

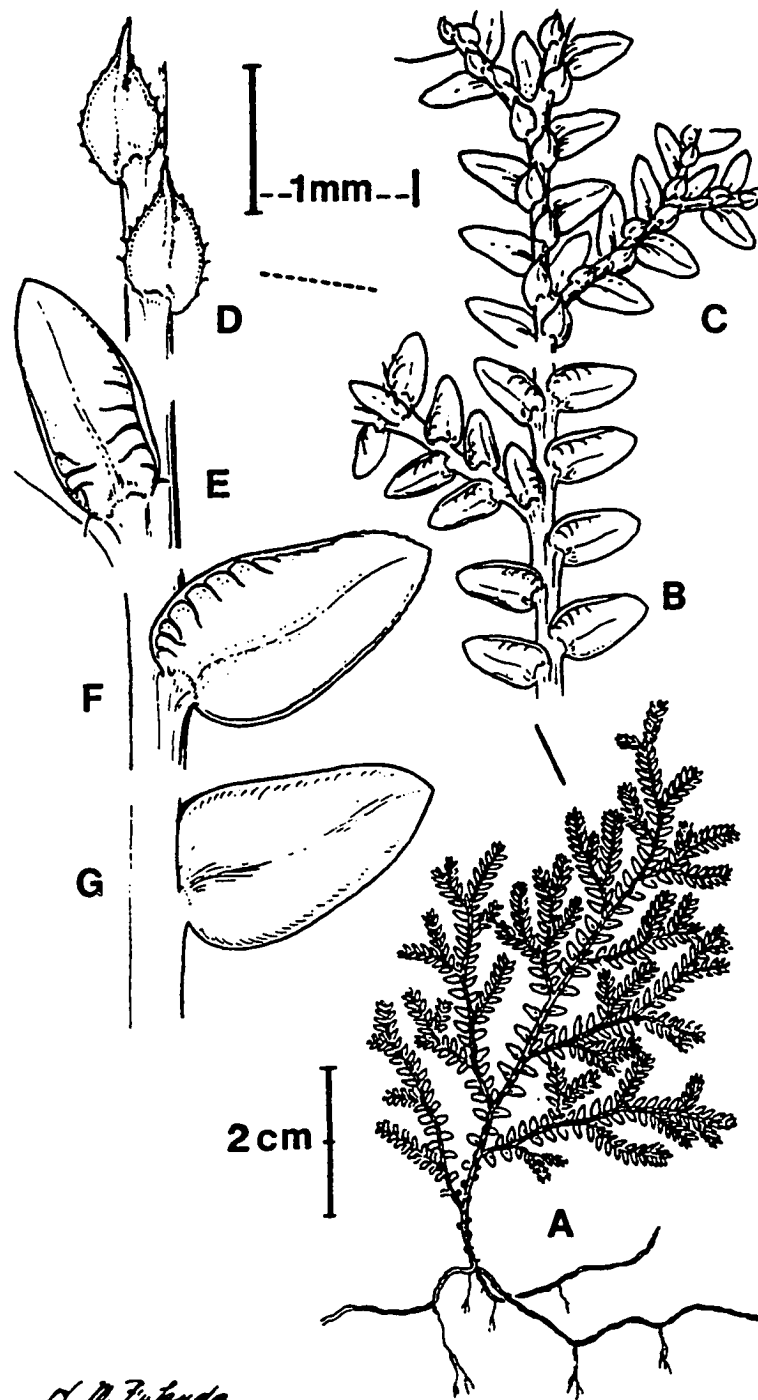
HABITAT AND DISTRIBUTION: Along waterway banks, road cuts, or on hillsides with limestone outcrops; 1327-2074 m; known only from the States of Oaxaca and Puebla, Mexico.

SPECIMENS EXAMINED: MEXICO. OAXACA: Juquila, along road to Puerto Escondido ca. 132 km S of Oaxaca, 21 Aug 1970, D. Norris & Taranto 16526a (NY); Sola de Vega, 20 km S of Sola de Vega, 6800 ft [2074 m], 6 Jun 1972, Hellwig & Whitaker 1269 (MEXU, NY), 26 km S of Sola de Vega, 5800 ft [1769 m], 6 Jun 1972, Hellwig & Whitaker 1272a (MEXU, NY), 35 km S of Sola de Vega, 4600 ft [1403 m], 6 Jun 1972, Hellwig & Whitaker 1277 (CAS, MICH, US); Sola de Vega, 35 km S of Sola de Vega, 21 km N of bridge at Juchatengo, 4350

ft [1327 m], 11 Aug 1971, Mickel 6300 (NY), 23-29 km S of Sola de Vega, 27-33 km N of bridge at Juchatengo, 5200-6200 ft [1586-1891 m], 11 Aug 1971, Mickel 6321 (NY, UC, type coll. of S. mixteca). PUEBLA: Zacatlán, 2040 m, 11 Jul 1925, Orcutt 1425 (DS).

TAXONOMIC DISCUSSION: Because of its suberect to erect and stoloniferous habit S. mixteca may be confused with S. prolifera, S. lineolata, S. finitima, and S. tuberosa. It differs from them chiefly by having long-ciliate to fimbriate, whitish or reddish scale-like leaves on the lowermost and underground parts of the stem, and pinard to baryta yellow megaspores.

Fig. 16. A-G. Selaginella mixteca (Mickel 6300, NY). A. Habit. B. Lower surface of branch. C. Upper surface of branch. D. Median leaves. E. Axillary leaf. F. Lateral leaf, lower surface. G. Lateral leaf, upper surface.



H. M. Fukuda

**22. *Selaginella prolifera* Valdespino, sp. nov. (Figs. 17A-E; Map 3).**

Type: MEXICO. OAXACA: Juchitán, Isthmus of Tehuantepec, 6 km S of Matías Romero, 600 ft [183 m], 27 Sep 1972, Mickel 6880 (Holotype: NY!; isotype: UC!).

A *S. flagellata* Spring foliis intermediis, lateralibus et sporophyllis ciliatis et superne idioblastis provisis diversa.

Etymology--L., prolifer, producing offsets, bearing progeny of offshoots; referring to the stolons found at the base of the stem from which new upright plants develop.

Plants terrestrial or epipetric. Stems suberect to erect, stramineous, 4-20 cm long, 0.28-0.6 mm diam., not articulate, not flagelliform, stoloniferous, 2- or 3-branched. Rhizophores axillary or axillary-ventral, restricted to basal  $\frac{1}{4}$  to  $\frac{1}{3}$  ( $-\frac{1}{2}$ ) of the stem, filiform, 0.16-0.24 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded cells with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, narrowly oblong to oblong-ovate,  $2-3 \times 0.9-1.4$  mm; the acroscopic base rounded to semicordate, strongly overlapping the stem, the basisopic base geniculate to geniculate-rounded, not overlapping the stem; the acroscopic margin narrowly

hyaline to pale green, long-ciliate along basal  $\frac{1}{2}$  to  $\frac{2}{3}$ , serrate apically, the basiscopic margin pale green, long-ciliate at proximal most base, otherwise entire to serrulate, especially apically, the basiscopic margin without conspicuous stomata; apex acute, dentate at tip; the upper surface glabrous, with idioblasts, without stomata, the lower surface glabrous, usually with conspicuous or obscure idioblasts, and with stomata along midrib. Median leaves distant, ascending, broadly ovate-elliptic or ovate-oblong,  $1.3-1.6 \times 0.66-1.2$  mm; base asymmetric, with the inner base truncate or rounded and the outer base with a well developed, long-ciliate auricle; margins hyaline, long-ciliate; apex abruptly long-aristate, the arista  $\frac{1}{2}$  or more the length of the lamina,  $0.46-0.68$  mm long, puberulent and dentate at tip, both surfaces glabrous, the upper surface with idioblasts, with stomata along midrib and occasionally with few scattered throughout the lamina, the lower surface without idioblasts and stomata. Axillary leaves lanceolate to lance-ovate; base rounded; margins pale green to hyaline, long-ciliate along basal  $\frac{1}{2}$  to  $\frac{2}{3}$ , serrate to serrulate apically; apex acute, dentate at tip. Strobili terminal on branch tips and stem apex, loosely quadrangular to weakly flattened,  $2-9$  mm long. Sporophylls slightly dimorphic; dorsal sporophylls green, spreading to ascending, basally attached to the axis, with a weakly developed adaxial flap extending along  $\frac{1}{4}$  to occasionally  $\frac{1}{2}$  the sporophyll length, asymmetric or ovate to ovate-lanceolate,  $0.9-1.4 \times 0.4-0.65$  mm, with a well developed, denticulate keel along midrib, the base rounded, the margins hyaline, short to moderately long-ciliate, the apex long-acuminate to aristate, the upper surface green, composed of  $\pm$  rounded

cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with idioblasts and usually conspicuous stomata throughout, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls pale green, ascending, pseudopeltately attached to the axis, with a weakly developed adaxial flap, ovate to ovate-lanceolate,  $0.9-1.4 \times 0.5-0.7$  mm, with a well developed, denticulate keel along midrib, the base rounded, the margins hyaline, short- to long-ciliate, the apex long-acuminate to aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present only on the lower surface. Megasporangia generally in two ventral rows or at the base of ventral rows, or infrequently absent; megaspores snow-white, without an equatorial flange or with a slightly developed one, the proximal face granulose-striate to granulose-reticulate with open reticulum of rather high ridges, the distal face reticulate with open reticulum of low to high ridges,  $220-255 \mu\text{m}$  diam. Microsporangia in two dorsal rows, frequently also on the apical region of ventral side of strobili, or strobili wholly microsporangiate; microspores not studied.

**HABITAT AND DISTRIBUTION:** On waterway banks, shaded roadside banks, or on moist rocky banks; 46-900 m; known only from Mexico and Nicaragua, and to be expected at low elevations at least on the Pacific slope of Guatemala, El Salvador, and Honduras (possibly even to Panama).



PARATYPES: MEXICO. CHIAPAS: Villa Corzo, 58 km S of Mexican Hwy 190 on road to Nueva Concordia, 900 m, 11 Sep 1974, Breedlove 37635A (DS).

GUERRERO: La Puerta, 100 m, 5 Oct 1898, Langlassé 421 (GH, MEXU, US).

OAXACA: Jamiltepec, 40 km SE of Pinotepa Nacional on Rte 200, 200 ft [61 m], 1 Oct 1972, Mickel 6891 (NY); Jamiltepec, 3 km E of Pinotepa Nacional on Rte 200, 500 ft [152 m], 1 Oct 1972, Mickel 6901 (NY); Jamiltepec, 5 km N of Rte 200 on Rte 125, 12 km NW of Pinotepa Nacional, 7 km S of Coxcatitlán, 118 km S of Putla, 700 ft [213 m], 1 Oct 1972, Mickel 6912 (NY, UC); Jamiltepec, 4-8 km N of Ixcapa, 91-95 S of Putla, 800-1600 ft [244-488 m], 1 Oct 1972, Mickel 6925 (NY); Juchitán, km 218.2 between Chivela and Almoloya, near Almoloya, 800 ft [244 m], 23 Jul 1972, Hallberg 1655 (NY); [Juchitán,] Almoloya (on Tehuantepec National Railway), 17 Jun 1910, Orcutt 5238 (DS); [Juchitán,] Almoloya, 100-250 m, Jul 1937, Ll. Williams 9800 (F); Juchitán, Isthmus of Tehuantepec, 11 km N of Matías Romero, 700 ft [213 m], 19 Oct 1969, Mickel 4192 (NY p.p., UC-2 sheets [one p.p.]); Juchitán, Isthmus of Tehuantepec, 6 km S of Matías Romero, 600 ft [183 m], 27 Sep 1972, Mickel 6880 (NY, UC, type coll. of S. prolifera); Juchitán, 9 km E of Tapanatepec on Rte 190, 7 km E of intersection of Rtes 190 & 200, 500 ft [152 m], 4 Aug 1971, Mickel 5972 (NY, UC); Juchitán, 122 km E of Tehuantepec on Rte 190, 10 km E of Zanatepec, km 78-79, 150 ft [46 m], 4 Aug 1971, Mickel 5987 (NY, UC); Juquila, 9-25 km N of Puerto Escondido, 350-700 ft [107-213 m], 10 Aug 1971, Mickel 6055 (NY, UC); Pochutla, 13 km N of Pochutla, 800 ft [244 m], 30 Sep 1970, Mickel 5128 (NY, UC), 5133b (NY, UC);

Pochutla, 18 km N of Pochutla, 700 ft [213 m], 30 Sep 1970, Mickel 5144 (NY, UC); 24 km S of San Gabriel, 700 ft [213 m], 7 Jun 1972, Hellwig & Whitaker 1319 (MEXU).

NICARAGUA. [Granada:] Mombacho, Jan 1847, Oersted 2078 (US). [Masaya:] Masaya, 250 m, 1-8 Nov 1911, A. Hitchcock (US); Laguna de Masaya and vicinity, ca. 300 m, 6 Jul 1923, Maxon 7745 (US); Laguna de Masaya and vicinity, ca. 300 m, 6 Jul 1923, Maxon 7750a (US-2 sheets).

NOMENCLATURAL COMMENTS: Mickel and Beitel (1988) treated most of the collections of S. prolifera from Oaxaca as S. rhizophora Baker. Upon examination of the type collection of the latter I concur with other authors (e.g., Alston, 1955; Lellinger, 1989; Smith, 1981) in concluding that S. rhizophora is conspecific with S. flagellata. Thus, specimens representing S. rhizophora as defined by Mickel and Beitel (1988) are in need of a name, which I provide here.

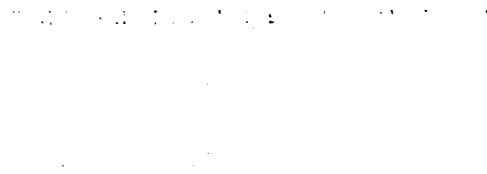
TAXONOMIC DISCUSSION: Selaginella prolifera differs from S. flagellata by having median and lateral leaves and sporophylls with ciliate (vs. serrate to serrulate) margins and the upper surface with (vs. without) idioblasts.

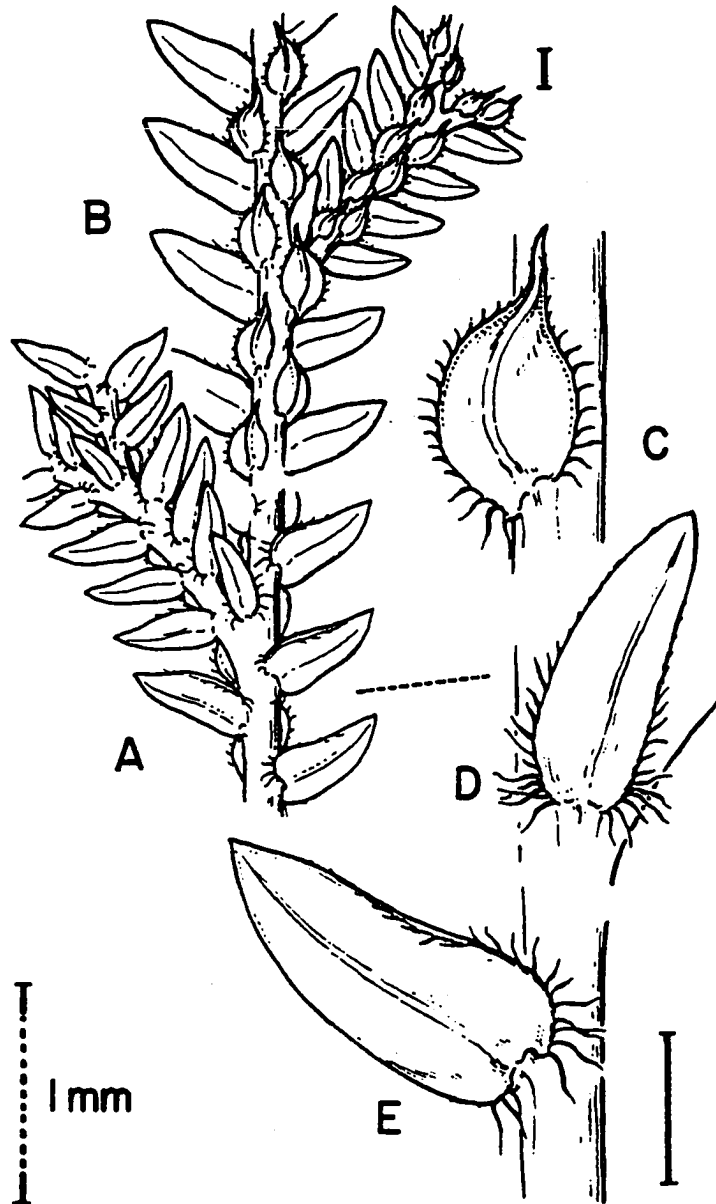
The upright stems in S. prolifera arise from underground to partially buried stolons. In addition to this characteristic, S. prolifera also agrees with other erect to suberect species such as S. lineolata, S. finitima, and S. tuberosa, in having the median leaves with an outer auricle and this suggests a close relationship among

these taxa. They all can be distinguished, however, by the characteristics given in the key.

Alston (1955) cited some specimens of S. prolifera either as S. hoffmannii Hieron. (i.e., Langlassé 421), or as S. novae-hollandiae (Sw.) Spring (i.e., A. Hitchcock). Both S. hoffmannii and S. novae-hollandiae lack idioblasts on the upper surface of the leaves.

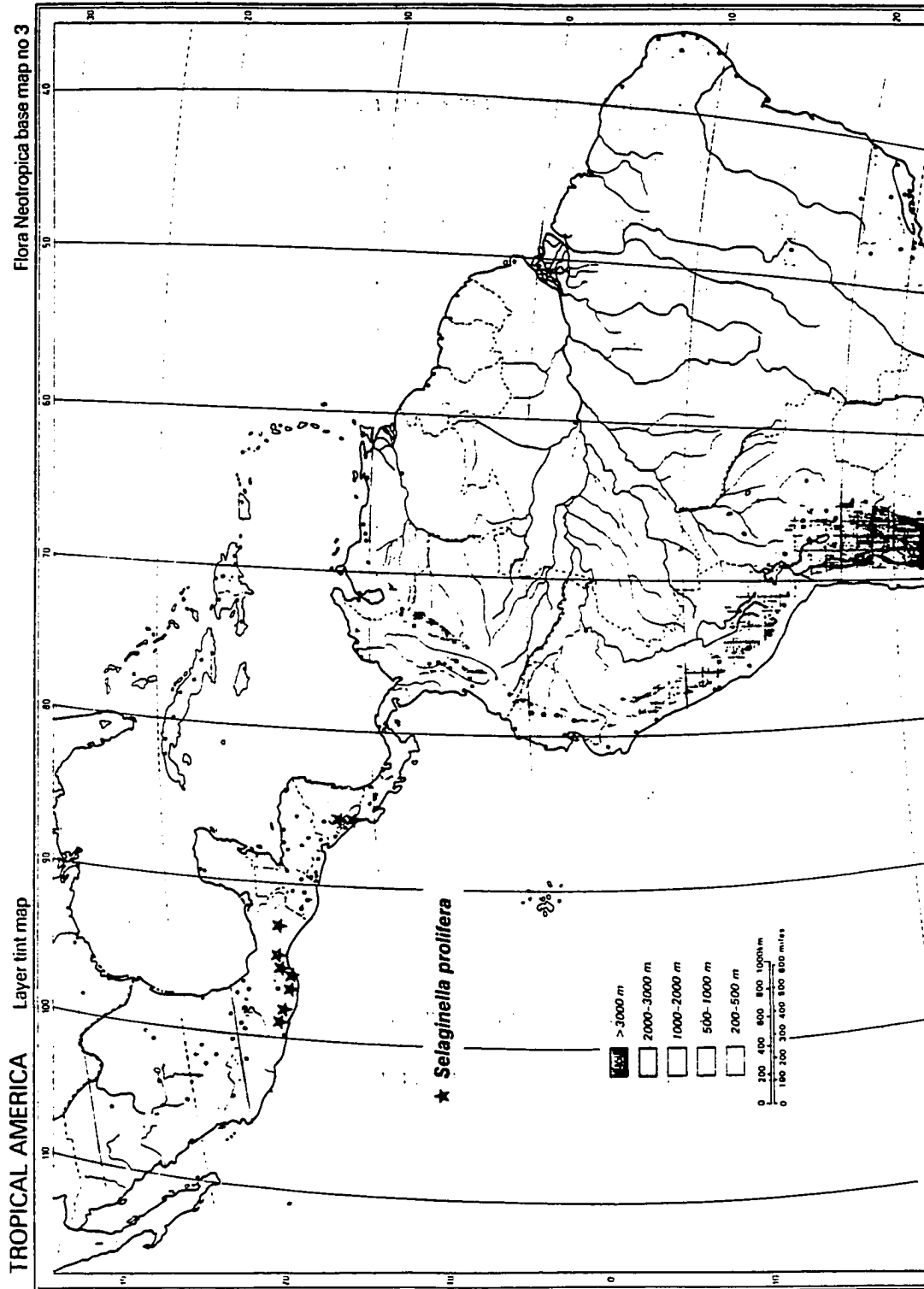
Fig. 17. A-E. Selaginella prolifera (Mickel 6880, NY). A. Lower surface of branch. B. Upper surface of branch. C. Median leaf. D. Axillary leaf. E. Lateral leaf.





*N. M. Fukuda*

Map 3.



**23. *Selaginella lineolata* Mickel & Beitel, Mem. New York Bot. Gard. 46: 343.**

1988. (Figs. 18A-D).

Type: MEXICO. OAXACA: Putla, 24 km N. of Putla, 4450 ft [1357 m], 11

Oct 1969, Mickel 4014 (Holotype: NY!; isotype: NY!).

Plants terrestrial or epipetric. Stems suberect to erect, stramineous, 4.5-33 cm long, 0.24-0.9 mm diam., not articulate, with flagelliform branch and stem apices, stoloniferous, 2- or 3-branched. Rhizophores axillary or axillary-ventral, restricted to basal  $\frac{1}{4}$  or throughout the stem on flagelliform plants, filiform, 0.08-0.26 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, broadly ovate, ovate-oblong, or oblong, 1.6-2.9  $\times$  0.9-1.7 mm; base rounded to subcordate, the acroscopic base strongly overlapping the stem, the basiscopic base auricled to rounded, with the auricle overlapping the dorsal side of stem; the acroscopic margin narrowly to widely hyaline or pale green, long-ciliate, ciliate-denticulate, or serrate along basal  $\frac{1}{3}$ , serrate to serrulate apically, the basiscopic margin narrowly hyaline or pale green, frequently long-ciliate at proximal most base and entire to serrulate or entire to serrulate throughout, the basiscopic margin without conspicuous stomata; apex broadly acute to acute, dentate at tip; the upper surface glabrous, with idioblasts and frequently with scattered stomata, the lower surface

glabrous, usually with conspicuous or obscure idioblasts, and with stomata along midrib. Median leaves distant, ascending, broadly ovate-elliptic, ovate-lanceolate, or ovate-oblong,  $0.8-1.75 \times 0.5-0.95$  mm; base asymmetric, with the inner base rounded or auricled, frequently ciliate, ciliate-denticulate, or entire, the outer base with a well developed, and long-ciliate or entire auricle; margins hyaline, serrate, ciliate denticulate, or the inner margin shortly ciliate and the outer margin serrate; apex gradually long-acuminate to long-aristate, the acumen or arista  $\frac{1}{2}$  or less the length of the lamina, 0.1-0.54 mm long, frequently puberulent, dentate at tip, both surfaces glabrous, the upper surface with idioblasts, with stomata along midrib and frequently scattered throughout the lamina, the lower surface without idioblasts and stomata. Axillary leaves similar to lateral leaves. Strobili terminal on branch tips and stem apex, lax and flattened, dorsiventral, 2-7 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{2}{3}$  or throughout the sporophyll length, asymmetric or lanceolate,  $1.1-2.25 \times 0.34-0.8$  mm, with a strongly developed, denticulate keel along midrib, the base rounded, the margins hyaline, shortly ciliate to serrate, the apex acute to shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with idioblasts and usually conspicuous stomata throughout, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, frequently with obscure idioblasts and stomata; ventral sporophylls hyaline to pale green,



ascending, pseudopeltately attached to the axis, without or with a weakly developed adaxial flap, ovate to ovate-lanceolate,  $0.9-1.7 \times 0.48-0.84$  mm, with a well developed, denticulate keel along midrib, the base rounded, the margins hyaline, ciliate-denticulate along basal  $\frac{2}{3}$ , serrate to serrulate apically, the apex long-acuminate to shortly aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present only on the lower surface. Megasporangia generally in two ventral rows or at the base of ventral rows, or infrequently absent; megaspores bone-white, with a slightly to moderately developed equatorial flange, the proximal face striate-reticulate with open reticulum of rather high ridges, the distal face reticulate with open to close reticulum of low ridges,  $275-340$   $\mu\text{m}$  diam. Microsporangia in two dorsal rows, frequently also on the apical region of ventral side of strobili, or strobili wholly microsporangiate; microspores not studied.

HABITAT AND DISTRIBUTION: On shaded slopes, limestone outcrops, sandy soil, or waterway banks; (250-)915-2470 m; Mexico and Guatemala.

SPECIMENS EXAMINED: MEXICO. COLIMA: SW foothills of Nevado de Colima, 1-1.5 mi above [S of] Hacienda San Antonio, 1200-1250, 11 Aug 1957, McVaugh 16097 (CAS, MICH, US). CHIAPAS: Cintalapa, on Oaxaca-Chiapas border near La Cienega de León, 1080-1230 m, 1 Dec 1980, Breedlove & Almeda 48159 (CAS p.p., ENCB p.p.). GUERRERO: 20 mi S of Chilpancingo, 16 Aug 1947,

Webster et al. 17M842 (F); ca. 14 km SSW del Campamento El Gallo, sobre el camino a Atoyac, estribaciones suroccidentales del Cerro Teotepec, ca. 17°25'N, 100°14'W, 1900 m, 26-27 Jan 1965, Rzedowski & McVaugh 26 (MICH). HIDALGO: Above San Pedrito near Agua Blanca, 6000 ft [1830 m], 28 Aug 1945, A. Sharp 45865 (MEXU p.p., US). JALISCO: Near Guadalajara, Sep 1889, Pringle 2593a (BR, GH, M, NY-2 sheets, P, US-2 sheets), 6 Oct 1891, Pringle 4037 (GH); Tala, Rancho Las Higueras, 1600 m, 4 Oct 1974, D. García (NY); Talpa, El Veladero, 1200 m, 24 Oct 1985, Sahagún 16184 (UC); Cerro de Tequila, 1600 m, 7 Sep 1985, E. Barcena [Barcena?] 17027 (UC); Zapopan, Los Camachos, 1400 m, 4 Oct 1974, C. Díaz 5446 (UC). MÉXICO: Ocuilán, barrancas de Ocuilán, 1930 m, 28 Sep 1985, Abundiz 234 (ENCB); Ocuilán, cañada de Ocuilán, 1930 m, 5 Oct 1984, Tejero 2012 (ENCB); Tejupilco, camino a Rincón Potrero, 980 m, 19 Oct 1986, Abundiz 306 (ENCB), 308 (ENCB); Temascaltepec, Ipericones, 24 Aug 1935, Hinton et al. 8212 (DS, GH, MEXU p.p., NY p.p., US); Zacualpan, Mamatla, 2290 m, 3 Jun 1984, Tejero 1985 (ENCB). NAYARIT: Mountains 9 mi N of Compostela, 1000-1200 m, 28 Aug 1957, McVaugh 16478 (MICH); hills 6-7 mi S of Compostela, 1000 m, 5 Sep 1960, McVaugh 18756 (CAS, MICH, NY); 9.5 mi W of Tepic, 1000-1100 m, 11 Sep 1960, McVaugh 18944 (MICH, NY); Tepic, along road to Jalcocotán, ca. 8 mi W of Hwy. 15, 6 Aug 1970, Norris & Taranto 15053 (ENCB, MICH). OAXACA: 35 km N of Ayutla along road from Mitla to Choapán, N slope of Cerro Zempoaltépetl, 2470 m, Breedlove & Sigg 65979 (CAS); Cuicatlán, vicinity of Teutila, 3000 ft [915 m], 25 Sep 1975, Mickel 7331 (NY); Matías Romero, 5 km

antes de Matías Romero sobre la carretera Acayucán-Matías Romero, 22 Oct 1980, Vovides & Perales 604 (XAL); Putla, 24 km N of Putla, 4450 ft [1357 m], 11 Oct 1969, Mickel 4014 (NY-2 sheets, type coll. of S. lineolata), 4019 (NY, UC). QUERETARO: Pinal de Amoles, 9 km S de Santa Agueda, sobre el camino a Ahuacatlán, 1150 m, 13 May 1988, Rzedowski 46613 (NY). SINALOA: 5 km N of El Palmito, 2300 m, 28 Oct 1973, Breedlove 35733 (CAS, MICH, MO); along Rte 40, 45 mi NE of jct. Rte 15 and 2.5 mi NE of Santa Lucia, 27 Jul 1972, McGill et al. 9555 (ENCB); 35 mi E of Villa Unión, 3500 ft [1067 m], 3 Sep 1967, Oliver et al. 744 (MO). VERACRUZ: Catemaco, Agaltepec Island, Lake Catemaco, 18°24'N, 95°05'W, 5 Aug 1976, Faden et al. 76/155 (UC); Huayacocotla, 1 km E of Viborillas, 4 km S of Huayacocotla, 1950-2100 m, 21 Jul 1982, Diggs & Nee 2905 (XAL); Orizaba, Mar 1856, M.B 88 (P); San Andrés Tuxtla, 10 Jan 1962, E. Schmid s.n. (Z), electricity plant, 11 Jan 1962, E. Schmid s.n. (Z); Tepetzintla, Sierra de Otontepec, 21°16'N, 97°52'W, 1250 m, 14 Dec 1981, G. Castillo et al. 2538 (XAL); barranca of Teoxolo near Jalapa, 3000 ft [915 m], 5 Jul 1906, Pringle 10806 (CAS, F, GH, MICH, UC, US-2 sheets).

GUATEMALA. QUETZALTENANGO: N of Sta. María de Jesús, 5800 ft [1769 m], 17 Jun 1972, Hellwig & Whitaker 1373 (F).

TAXONOMIC DISCUSSION: Selaginella lineolata has glabrous laterai and median leaves with conspicuous idioblasts, and white megaspores, which distinguish it from some of the other erect to suberect taxa with stoloniferous stems and

flagelliform branches, e.g., S. bernoullii and S. porphyrospora.

Selaginella lineolata is closely related to S. prolifera, S. finitima (see discussion under it), and S. tenella (syn.: S. cladorrhizans A. Braun). It can be distinguished from S. finitima by having idioblasts on the upper surface of both median and lateral leaves, flagelliform stem and branch apices, and conspicuous idioblasts and stomata on the upper surface of the dorsal sporophylls. Selaginella lineolata differs, besides other characteristics aforementioned under S. prolifera, from it by having flagelliform stem and branch apices, and a small, round auricle at the basiscopic base of the lateral leaves, and by the short ciliate-denticulate projections on the acroscopic margin of the lateral leaves, which are less than  $\frac{1}{4}$  the width of the lamina (vs. more than  $\frac{1}{3}$  or even  $\frac{1}{2}$  in S. prolifera).

Selaginella tenella differs from S. lineolata by the median leaves elliptic to ovate-elliptic, with the base oblique without a definite outer auricle, leaves generally with broad hyaline margins, and sporophylls slightly dimorphic. In addition, S. lineolata has basal stolons from which the upright stems develop, whereas these are absent in S. tenella, and in Mexico where the two overlap it is more robust than S. tenella.

In Mexico, the ciliate-denticulate leaves with conspicuous idioblasts of S. lineolata resemble those of S. stenophylla, but S. stenophylla can be distinguished by suberect habit, stout rhizophores, absent stolons, and more elongate lateral leaves, broadest at the base. The difference in the lateral leaf size and shape is especially conspicuous when the large stem leaves are compared. In S. lineolata

lateral leaves of the main stem are 2-2.5 mm long, whereas in S. stenophylla they are 3-3.5 mm long.

A specimen of S. lineolata from Veracruz, Pringle 10806 (CAS, F, GH, MICH, UC, US), is slightly different from typical ones by its more compact habit, lateral leaves perpendicular to the stem for most parts of the stem length, obscure idioblasts, and in general the acroscopic margin of the lateral leaves is more obviously long-ciliate. Otherwise, it falls within the present circumscription of S. lineolata. Specimens from Chiapas were among the tallest observed. One of them, Breedlove & Almeda 48159 (CAS p.p., ENCB p.p.), is atypical by its almost quadrangular to weakly flattened strobili, upper sporophylls not distinctly larger than the lower sporophylls, the lateral leaves with few short to long hairs at the basalmost portion of the basiscopic margin, and median leaf base with two rather well developed and long-ciliate auricles. In these last characters it resembles a non-member of subg. Heterostachys, S. hoffmannii Hieron. Red stem color was reported in living plants of S. lineolata [Hellwig & Whitaker 1373 (NY)], but this color fades on drying. Reddish to pink stems are typical of S. hoffmannii. This raises the possibility that S. lineolata may be somehow related to S. hoffmannii or may cross with it. This may explain why Breedlove & Almeda 48159 has some characteristics that resemble S. hoffmannii. That specimen differs from S. hoffmannii by its conspicuous to obscure idioblasts on the upper surface of the lateral leaves (vs. lacking), the stems stramineous when adult (vs. usually reddish to pink or occasionally stramineous), and stoloniferous leaves non-green or hyaline

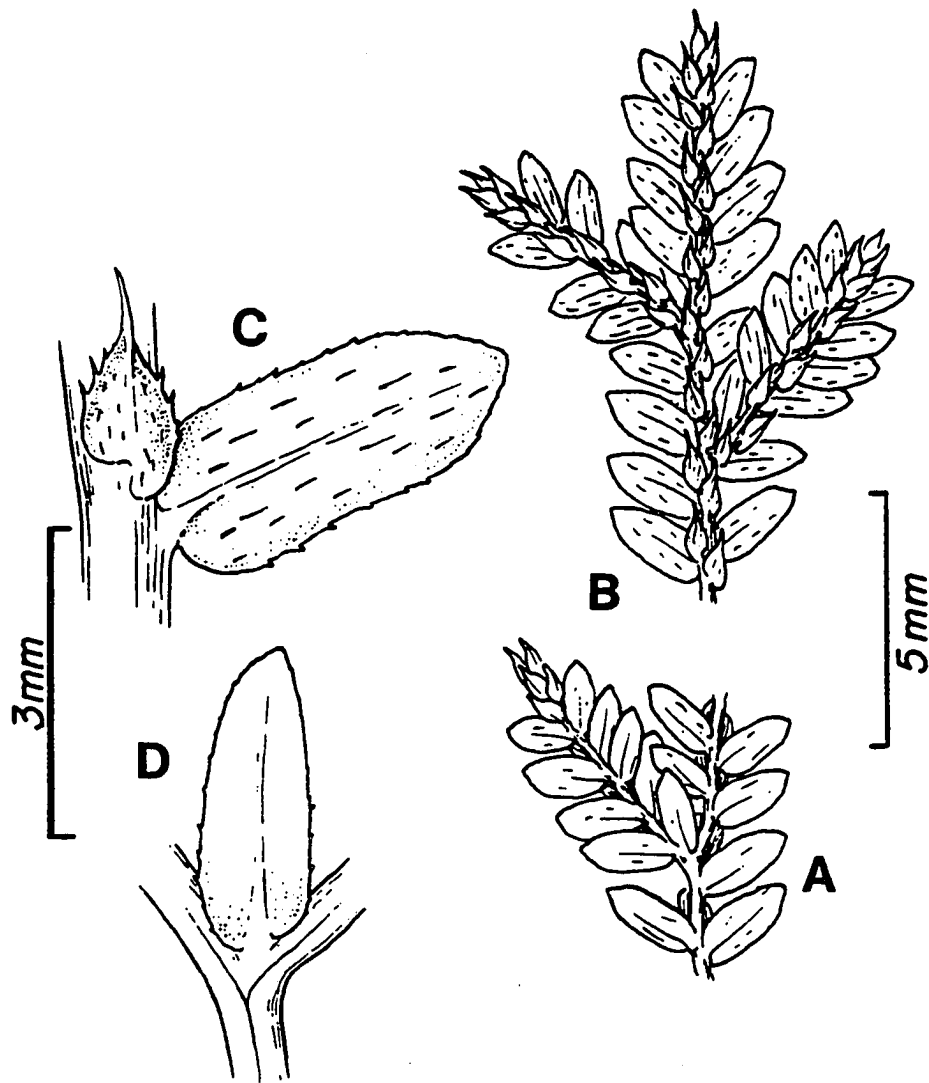
(vs. red-green). In general the median and lateral leaves of this collection fall within the morphological range of S. lineolata. Perhaps it represents an isolated population that deserves taxonomic recognition. I hesitate in recognizing it, however, because of the lack of additional collections. In addition, it is also possible that it represents only a form of the typical S. lineolata, which is rather variable in such characters as ciliation of leaf margins, size of the plants, and in possessing conspicuous or obscure idioblasts.

Some of the collections here cited from the state of México, Abundiz 234 (ENCB) and Tejero 2012 (ENCB), were previously referred by Abundiz and Tejero (1990) to S. hoffmannii.

The following collections treated under S. lineolata by Mickel and Beitel (1988) are referred here to S. tenella (P. Beauv.) Spring: Feddema 2517 (MICH); Hinton 8502 (NY); McVaugh & Koelz 1727 (MICH); Mexia 1276 (MICH-2 sheets, NY); Mexia 8725 (NY, UC); Mexia 8755 (NY).

Pringle 2593 (here cited as Pringle 2593a) has been found to represent or to be mixed with S. porphyrospora in different herbaria.

Fig. 18. A-D. Selaginella lineolata (Mickel 4014, NY). A. Lower surface of branch, with strobilus. B. Upper surface of branch, with strobilus; note idioblasts on the upper surface of the leaves. C. Median and lateral leaves; note idioblasts on the upper surface. D. Axillary leaf.



ROBBI ANGEL



**24. *Selaginella finitima* Mickel & Beitel, Mem. New York Bot. Gard. 46: 338.**

1988.

**Type:** MEXICO. VERACRUZ: Minantitlán, 6.6 km N de la terracería La Laguna-Río Grande, sobre el camino nuevo a Ejido Belisario Domínguez, 14.7 km al E de La Laguna, 17°20'N, 94°22'W, 130 m, 13 Julio 1980, Wendt & Villalobos 2543 (Holotype: NY!; isotypes: CAS!, MO!).

Plants terrestrial or epipetric. Stems suberect to erect, stramineous or greenish, 6-32 cm long, 0.36-0.86 mm diam., not articulate, occasionally with flagelliform stem and branch apices, stoloniferous, 2- or 3-branched. Rhizophores axillary, restricted to lowermost base or throughout the stem on flagelliform plants, stout to filiform, 0.12-0.4 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, broadly ovate or ovate-oblong,  $1.5-3.2 \times 1.2-2.1$  mm; base rounded to subcordate, the acroscopic base strongly overlapping the stem, the basiscopic base rounded to truncate, not overlapping the stem; the acroscopic margin narrowly to widely hyaline or pale green, short- to long-ciliate or serrate along basal  $\frac{1}{2}$ , serrate to serrulate apically, the basiscopic margin greenish, entire to serrulate or long-ciliate along basal  $\frac{1}{2}$  and serrate apically on basal stem leaves, the basiscopic margin without conspicuous stomata; apex rounded, obtuse, or broadly acute, dentate at

tip; the upper surface glabrous, without idioblasts, with or without obscure and scattered stomata, the lower surface glabrous, usually without idioblasts, with stomata along midrib. Median leaves distant, ascending, broadly elliptic or elliptic-orbicular,  $1.2-1.64 \times 0.7-1.0$  mm; base asymmetric, with the inner base truncate and entire, the outer base with a well developed and ciliate or denticulate auricle; the inner margin hyaline, the outer margin greenish along basal  $\frac{1}{2}$ , hyaline along apical  $\frac{1}{2}$ , both margins short-ciliate, ciliate-denticulate, or serrate; apex gradually or abruptly long-aristate, the arista less than  $\frac{1}{2}$  the length of the lamina, 0.15-0.35 mm long, frequently puberulent, dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib, the lower surface without idioblasts or stomata. Axillary leaves similar to lateral leaves, except more narrowly ovate and shortly ciliate to ciliate-denticulate along basal  $\frac{1}{2}$ . Strobili terminal on branch tips and stem apex, lax and flattened, dorsiventral, 2-10 mm long. Sporophylls slightly dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{1}{2}$  to  $\frac{3}{4}$  throughout the sporophyll length, asymmetric, ovate, or ovate-lanceolate,  $1.18-1.4 \times 0.48-0.74$  mm, with a well developed, denticulate keel along midrib, the base rounded, the margins hyaline, ciliate-denticulate basally, serrate apically, the apex acute, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts and frequently with conspicuous stomata throughout, the lower surface silvery green, composed of elongate cells with

sinuate walls, glabrous, frequently without obscure idioblasts or stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis, without or with a weakly developed adaxial flap, ovate to ovate-lanceolate,  $0.94-1.32 \times 0.44-0.74$  mm, with a well developed, denticulate keel along midrib, the base rounded, the margins hyaline, ciliate-denticulate throughout or serrate apically, the apex acute to short-acuminate, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present only on the lower surface. Megasporangia generally occupying basal half of two ventral rows or occasionally absent; megaspores cream, with an equatorial flange, the proximal face rugose, the distal face rugose-reticulate with close reticulum of low ridges,  $150-250 \mu\text{m}$  diam. Microsporangia in two dorsal rows and along apical  $\frac{1}{2}$  of ventral rows, or strobili wholly microsporangiate; microspores not studied.

**HABITAT AND DISTRIBUTION:** On limestone rocks and stream banks in wet lowland forests; 130-760 m; known only from Chiapas, Oaxaca, Tabasco, and Veracruz in Mexico.

**SPECIMENS EXAMINED:** MEXICO. CHIAPAS: La Independencia, 45-50 km E of Lagos de Montebello National Park, on road to Ixcan from Santa Elena, 760 m, 22 Jan 1982, Breedlove & Almeda 57707 (CAS); Palenque, Agua Azul, 300 m, 24 May 1973, Breedlove 35378 (DS), 35379a (DS, ENCB, NY); [Palenque,] along

trail behind Naranjo, 8 km from ruins of Palenque, 4 Mar 1975, Hoover 160 (MO); without data, G. Münch (DS). OAXACA: Sta. María de Chimalapa, Río Uxpanapa, entre La Gringa y el límite con Veracruz, 17°08'30"N, 94°07'30"W, 200 m, 27 Sep 1980, Wendt et al. 2758-A (MEXU, NY). TABASCO: Teapa, Cerro El Madrigal, Campo Experimental de Chapingo en Puyacatengo, 15 Aug 1989, Magaña & Lorea 2166 (ENCB). VERACRUZ: Hidalgotitlán, km 3 del camino Cedillo-La Laguna, 150 m, 19 Jan 1975, Dorantes 3970 (XAL); Minantitlán, 6.6 km N de la terracería La Laguna-Río Grande, sobre el camino nuevo a Ejido Belisario Dominguez, 14.7 km al E de La Laguna, 17°20'N, 94°22'W, 130 m, 13 Julio 1980, Wendt & Villalobos 2543 (CAS, MO, NY, type coll. of S. finitima).

TAXONOMIC DISCUSSION: Because of its similar distribution, median leaves with an outer auricle, which is frequently ciliate, suberect to erect habit, stoloniferous stem bases, and the frequently ciliate lateral leaves, S. finitima can be confused with S. prolifera and S. lineolata. Selaginella finitima differs chiefly from the other two species by lacking idioblasts on the upper surface of the leaves and sporophylls, by having the lateral leaves with a rounded, obtuse, or broadly acute apex, and the two halves of the leaves symmetric (vs. asymmetric in S. prolifera and S. lineolata).

As pointed out by Mickel and Beitel (1988), the specimen from Chiapas, Breedlove 35379 (here 35379a), was previously cited by Smith (1981) as S. novae-hollandiae. That species usually has acute lateral leaves with asymmetric halves,

and usually yellow megaspores (not cream as in S. finitima).

Some specimens of S. finitima (e.g., Wendt & Villalobos 2543, MO, NY, and Breedlove 35379a, DS, ENCB, NY) develop vegetative growth from the tips of strobili. In addition, Wendt & Villalobos 2543 (type coll.), possesses leafy rhizophores. This feature lends support to the view that rhizophores are modified shoots capable of developing leaves, but that usually bear roots at the tip.

**25. *Selaginella tuberosa* McAlpin & Lellinger, Brenesia 24: 409. 1985 [1986].**

(Map 1).

Type: COSTA RICA. PUNTARENAS: Las Alturas de Cotón, ca. 4000 ft [1220 m], 25 Aug 1974, McAlpin 2505 (Holotype: US-n.v.; isotypes: CR-n.v., DUKE-n.v., F!, NY!).

Plants terrestrial or occasionally epipetric. Stems suberect to erect, stramineous, 10-30 cm long, 0.5-1.4 mm diam., not articulate, not flagelliform, stoloniferous with tuber-like buds at the tip, (2-)3-branched. Rhizophores axillary or axillary-ventral, restricted to basal  $\frac{1}{4}$ , filiform, 0.1-0.3 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, broadly ovate, ovate-oblong, or oblong,  $2.8-4.5 \times 1.6-2.5$  mm; the acroscopic base rounded, slightly or not overlapping the stem, the basiscopic base geniculate to truncate; the acroscopic margin greenish to narrowly hyaline, moderately long-ciliate along basal  $\frac{1}{3}$ , serrate to serrulate apically, the basiscopic margin greenish to pale green, long-ciliate at proximal base, otherwise serrulate throughout, the basiscopic margin without conspicuous stomata; apex acute, broadly acute, or obtuse, dentate at tip; the upper surface glabrous, without idioblasts or these inconspicuous, without conspicuous stomata, the lower surface glabrous, usually without conspicuous idioblasts, with stomata

along midrib. Median leaves distant, ascending, broadly elliptic,  $1.8-3.5 \times 1.28-1.6$  mm; base auricled, with an inner and outer auricle, the auricles long-ciliate, the outer auricle slightly longer than the inner one; margins narrowly hyaline, serrulate; apex abruptly short- to long-aristate, the arista  $\frac{1}{2}$  or less the length of the lamina, 0.3-0.9 mm long, frequently puberulent, dentate at tip, both surfaces glabrous, the upper surface with conspicuous idioblasts, with stomata along midrib and scattered throughout the lamina, the lower surface without idioblasts and stomata. Axillary leaves similar to lateral leaves or more oblong. Strobili terminal on branch tips, lax and flattened, dorsiventral, 2-4 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{1}{2}$  to  $\frac{3}{4}$  the sporophyll length, asymmetric, lanceolate or lance-ovate,  $1.68-2.6 \times 0.58-0.9$  mm, with a strongly developed, denticulate keel along midrib, the base rounded, the margins hyaline, shortly ciliate basally, otherwise ciliate-denticulate to serrate apically, the apex acute to shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with idioblasts and conspicuous stomata throughout, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, frequently with obscure idioblasts and stomata; ventral sporophylls pale green, ascending, pseudopeltately attached to the axis, with a weakly developed adaxial flap, ovate to ovate-lanceolate,  $1.84-2.32 \times 0.9-1.14$  mm, with a well developed, denticulate keel along midrib, the base rounded, the

margins hyaline, ciliate-denticulate basally, serrate to serrulate apically, the apex long-acuminate to shortly aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present only on the lower surface. Megasporangia seemingly only a single one at the base of the ventral sporophyll rows; megaspores not well observed, white to bone-white, seemingly without an equatorial flange, the proximal face not readily observed, the distal face reticulate with seemingly close reticulum of low ridges, not measured. Microsporangia occupying almost the entire strobili; microspores immature.

HABITAT AND DISTRIBUTION: On soil in coffee plantations, waterway banks, road banks, or rocky slopes in premontane forest with a pronounced dry season (McAlpin & Lellinger, 1985 [1986]); 1100-1900 m; Mexico and Costa Rica, and to be expected throughout Central America.

SPECIMENS EXAMINED: MEXICO. OAXACA: Juquila, 28-29 km N of San Gabriel, 4500-4700 ft [1372-1433 m], 10 Aug 1971, Mickel 6193 (NY).

COSTA RICA. PUNTARENAS: Along trail between Las Alturas and Cotonsito, along Río Cotón, 8°56'30"N, 82°[83°?]48'W, 1400 m, 31 Aug-1 Sep 1983, Davidse 24646 (UC); Las Alturas and vicinity, 1400 m, 26 Aug 1974, Maas & McAlpin 1477 (F); Las Alturas de Cotón, ca. 4000 ft [1220 m], 25 Aug 1974, McAlpin 2505 (F, NY, type coll. of S. tuberosa); cultivated at NY, originally from Las Alturas, Dec. 1976, McAlpin (US); Cerro de San Isidro near San Ramón,



1300 m, 14 Jun 1901, Brenes 14495 (GH, US). SAN JOSÉ: Río Tiribí, 1100 m, Aug 1906, Biolley 17002 (P). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Tablazo, 9 Sep 1906, Biolley 108 (US).

TAXONOMIC DISCUSSION: Selaginella tuberosa is easily distinguished from other species that have the median leaves with a ciliate and well developed outer auricle, by having the lateral leaves with the midrib raised and frequently hyaline, and the median leaves with a well developed, long-ciliate inner auricle.

McAlpin and Lellinger (1985) speculated that S. tuberosa was closely related to S. sylvestris Asplund, a member of the articulate species of the genus. Contrary to McAlpin and Lellinger (1985), I have found that S. tuberosa has axillary or axillary-ventral (not dorsal) rhizophores, lacks stem articulations, and all other characteristics that define series Articulatae (see Valdespino, 1993a, for a discussion on these characteristics). Because of its lax, flattened and dorsiventral strobili, dimorphic sporophylls, dorsal sporophylls with a laminal flap, idioblasts on the upper surface of the median leaves, and frequently bluish green leaves, I consider S. tuberosa as belonging to subg. Heterostachys, and accordingly it is treated here.

Two specimens of S. tuberosa, Biolley 108 (US) and Brenes 14495 (US), were cited by Alston (1955) as S. novae-hollandiae. Selaginella tuberosa is easily distinguished from it by the characters given above.

**26. *Selaginella macilenta* Baker, J. Bot. 22: 90. 1884.**

Type: ECUADOR. [CHIMBORAZO:] At the foot of Mt. Chimborazo, 3000 ft [915 m], [Jun 1860,] Spruce (Holotype: K!; probable isotype: P!).

Plants terrestrial, epipetric, or epiphytic. Stems creeping, greenish or stramineous, 3-7 cm long, 0.12-0.4 mm diam., not articulate, with flagelliform stem and branch apices, stoloniferous, 1- or 2-branched. Rhizophores axillary, restricted to basal ½ or throughout the stem, filiform, 0.04-0.1 mm diam. Leaves dimorphic throughout, thin-membranous, the upper surface green, composed of polygonal to ± rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, broadly ovate or ovate-oblong, 1.6-2.7 × 0.9-1.6 mm; base rounded, the acroscopic base slightly to strongly overlapping the stem, the basiscopic base not overlapping the stem; margins greenish, the acroscopic margin serrate to ciliate-denticulate along basal ½, serrulate apically, the basiscopic margin serrulate, without conspicuous stomata; apex acute, dentate at tip; the upper surface glabrous, without idioblasts or stomata, the lower surface glabrous, usually with conspicuous idioblasts, and with stomata along midrib. Median leaves distant, ascending, broadly elliptic or obovate-elliptic, 0.56-1.2 × 0.4-0.7 mm; base asymmetric to oblique, with the outer base subventricose, frequently with short cilia or teeth; margins greenish to pale green, serrate to serrulate; apex abruptly aristate, the arista ⅓ or less the length of the lamina, 0.14-0.3 mm long, frequently

puberulent, dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib and frequently along the basal  $\frac{1}{2}$  near the outer margin, the lower surface without idioblasts or stomata. Axillary leaves similar to lateral leaves. Strobili terminal on branch tips, lax and flattened, dorsiventral, 2-6 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{1}{3}$  to  $\frac{3}{4}$  the sporophyll length, asymmetric or lanceolate,  $1.1-1.76 \times 0.32-0.7$  mm, with a well developed, denticulate to entire keel along midrib, the base rounded, the margins narrowly hyaline, serrate to serrulate, the apex acute, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts, with stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis, without an adaxial flap, ovate-lanceolate to ovate,  $0.96-1.3 \times 0.32-0.56$  mm, with a slightly developed, denticulate to entire keel along midrib, the base rounded, the margins narrowly hyaline, serrate to serrulate, or occasionally ciliate-denticulate, the apex acute to short-acuminate, both surfaces composed of elongate cells with sinuate walls, glabrous, with obscure idioblasts, the stomata present only on the lower surface along the midrib. Megasporangia frequently absent, or in two ventral rows or at the base of ventral rows, or infrequently absent; megaspores snow-white, seemingly without an equatorial

flange, the proximal face seemingly smooth to rugulate, the distal face seemingly rugulate-reticulate with open reticulum of low ridges, 240-260  $\mu\text{m}$  diam. Microsporangia in two dorsal rows, frequently also on the apical region of ventral side of strobili, or strobili wholly microsporangiate; microspores not studied.

**HABITAT AND DISTRIBUTION:** On shaded forest floor, forested cliffs, wet road banks, mossy rocks, rocky stream banks, or on trees; 800-2200 m; Ecuador and Peru.

**SPECIMENS EXAMINED:** ECUADOR. **COTOPAXI:** Quevedo-Latacunga road, 0°55'S, 79°10'W, 800-950 m, 5 Apr 1973, Holm-Nielsen et al. 2994 (F, MO, NY, S), along Río Pilaló, 0°53'S, 79°10', 950-1100 m, 6 Apr 1973, Holm-Nielsen et al. 3104 (F, MO, NY, S). [CHIMBORAZO:] At the foot of Mt. Chimborazo, 3000 ft [915 m], [Jun 1860,] Spruce (K, P, type coll. of S. macilenta). **PICHINCHA:** Reserva Florística-Ecológica "Río Guajalito," km 59 de la antigua carretera Quito-Sto. Domingo de Los Colorados, 3.5 km NE de la carretera, estribaciones occidentales del Volcán Pichincha, 0°13'53"S, 78°48'10"W, 1800-2200 m, 10 Aug 1985, J. Jaramillo & Zak 7970 (AAU-2 sheets, QCA); Estación Biológica Río Guajalito, Quebrada Las Palmeras, km 59 along road Chillogallo-Alluriquín, 0°14'S, 78°47'W, 1800-2000 m, 30 Nov 1991, Ollgaard 99954 (AAU); road Guala-LA Armenia, 3 km from La Armenia, 0°06'N, 78°43'W, 1800 m, 3 May 1982, Ollgaard 37865, 37901, 37928 (AAU); old road Quito-Santo Domingo, SW of Chiriboga, km 89-90

from Quito, 0°20'S, 78°52'W, 1100 m, 8 Jul 1979, B. Løjtnant & Molau 15641 (AAU, QCA); Quito-Mindo road, 5000 ft [1525 m], 18 May 1958, Prescott 1449 (NY); Río Toachi, above the confluence with the Río Pilatón, 3000 ft [915 m], 4 Apr 1951, Bell 227 (BM, GH, RB, S); Solaya, W de la Cordillera Occidental, 1800 m, 9 Sep 1943, Acosta 5790 (US).

PERU. JUNÍN: Chanchamayo, 750 m, 3 Sep 1960, Kunkel 347 (S).

COUNTRY UNKNOWN: (ECUADOR?) San Florencio?, André K1810 (K).

TAXONOMIC DISCUSSION: Selaginella macilenta is an insufficiently known species that is characterized by its creeping habit, thin-membranous leaves, the median leaves elliptic or obovate-elliptic with an abruptly aristate apex, and flagelliform stem and branch apices. Because of its flagelliform stem and branch apices, the shape of the lateral leaves, and the snow-white megaspores, I believe S. macilenta to be closely related to and difficult to separate from S. flagellata.

I have noticed that strobilar tips of S. macilenta occasionally develop vegetative growth in the form of a long, flagelliform stem. This type of vegetative growth from the apex of the strobilus has been observed in other species treated in this monograph, including S. flagellata.

In general, S. macilenta can be distinguished from S. flagellata by having a more delicate texture and median leaves with an abruptly (vs. gradually) aristate apex, which is ca.  $\frac{1}{3}$  or less (vs. at least  $\frac{1}{2}$  or more) the length of the lamina.

Alston et al. (1981) cited Alston 7293 (BM) as S. macilenta, but upon examination I have determined that it is actually S. flacca.

**27. *Selaginella flagellata*** Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 228. 1843.

(Figs. 9E & F; 19A-F; Map 4).

Type: "GUYANA GALLICA" [FRENCH GUIANA]. Ad rivulus Oyapok superioris [upper Oyapok river], [Jun,] Leprieur (Lectotype: G!, here designated; isoelectotypes: B!, P-2 sheets!; probable isoelectotypes: GH!, P-3 sheets!, US!).

*Selaginella ambigua* A. Braun, Ann. Sci. Nat. Bot. V, 3: 286. 1865.

Syntypes: VENEZUELA. [ARAGUA: Colonia Tovar,] Fendler [324] p.p. (B!, GH!, MO!, YU!). [SUCRE: Quebrada del Imposible,] Cumaná, Moritz 221 (B!).

*Selaginella leptostachya* A. Braun, Ann. Sci. Nat. Bot. V, 3: 289. 1865.

Type: COLOMBIA. [BOYACÁ]: Muzo Minas, 700 m, Lindig 1514 (Holotype: B!; isotypes: BM!, K!, fragment NY!, P!, fragment US!).

*Selaginella regularis* Baker, J. Bot. 22: 277. 1884.

Type: PERU. [SAN MARTÍN]: Eastern Peru, near Tarapoto, [1855-1856], Spruce 3977 (Holotype: K!, fragment B!; isotypes: BM!, BR!, E!, OXF!, W!).

*Selaginella rhizophora* Baker, J. Bot. 22: 244. 1884.

Syntypes: PANAMA. PANAMÁ: "In woods near the towns of San Juan and Panama" [in sylvis prope Villa] San Juan, Oct 1846], Seemann 29 (K!); [in sylvis prope urbe Panama, Nov 1846,] Seemann 32 (fragment B!, K!).

*Selaginella reptans* Sodirol, Crypt. Vasc. Quit. 597. 1893.

Syntypes: ECUADOR. MANABI, Río Toachi, Sodiro (P!); San Miguel de Los Colorados, Sodiro (P-n.v.) [both, fide Alston et al., 1981: 273].

WITHOUT SPECIFIC LOCALITY: Sodiro [?] (not located).

Selaginella ambigua A. Braun var. fallax Hieronymus, Hedwigia 58: 317. 1917.

Syntypes: TRINIDAD. Jenman 7 (3456) (B!, NY!); 1877-1878, Fendler 42 (B!, BM!, GH!, KI, M, NY-5 sheets!, S!, UC!, US!, YU!).

Selaginella ambigua A. Braun var. minor Hieronymus, Hedwigia 58: 316. 1917.

Syntypes: TRINIDAD. Ex reliquiis Cruegerianis, Purdieanis etc. 186 (B-2 sheets!), 187 (B!), 189 (B!), 192 (B!), 193 (B-2 sheets!).

Selaginella othmeri Hieronymus, Hedwigia 58: 324. 1917.

Syntypes: TRINIDAD. "Avantille-valley" in declivibus siccis, 14 Dec 1903, Othmer 185 (B-2 sheets!, M-2 sheets!); in montibus Santa Cruz, 5 Dec 1907, Broadway 1988 p.p. (B!); "Santa Cruz," 1908, Broadway 3286 (B-2 sheets!, NY!).

Selaginella purdiei Hieronymus, Hedwigia 58: 322. 1917.

Type: TRINIDAD. 1877-1878, Fendler 42 p.p. (Holotype: B!).

Plants terrestrial, epipetric, or epiphyte. Stems suberect to erect, stramineous, 6-15 cm long, 0.2-1 mm diam., not articulate, frequently with flagelliform stem apex, stoloniferous or not, 2-4-branched. Rhizophores axillary, restricted to basal 1/3 or throughout the stem on flagelliform plants, filiform to moderately stout, 0.05-0.5 mm diam. Leaves dimorphic throughout, membranous,



the upper surface green, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, broadly ovate, ovate-lanceolate, or ovate-oblong,  $2.5 \times 1.3$  mm; base rounded to semicordate, the acroscopic base strongly overlapping the stem, the basiscopic base rounded, not overlapping the stem; the acroscopic margin narrowly hyaline or pale green, serrate along basal  $\frac{1}{3}$ , serrate to serrulate apically, the basiscopic margin narrowly hyaline or pale green, entire to serrulate apically; apex acute, dentate at tip; the upper surface glabrous, without idioblasts or conspicuous stomata, the lower surface glabrous, usually with conspicuous or obscure idioblasts, and with stomata along midrib. Median leaves distant, ascending, elliptic or broadly ovate-elliptic,  $1.2 \times 0.5-1.7$  mm; base oblique or asymmetric with the inner base truncate to rounded, entire, the outer base frequently with a weakly developed, entire auricle; margins hyaline, serrate to serrulate; apex long-acuminate to long-aristate, the acumen or arista  $\frac{1}{4}-\frac{1}{2}$  the length of the lamina, 0.4-1 mm long, frequently puberulent, dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib, the lower surface without idioblasts or stomata. Axillary leaves similar to lateral leaves. Strobili terminal on branch tips and stem apex, lax and flattened, dorsiventral, 0.2-5 cm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending  $\frac{2}{3}$  or throughout sporophyll length, asymmetric or lanceolate,  $1.2-2 \times 0.4-0.9$  mm, with a strongly developed,

denticulate keel along midrib, the base rounded, the margins hyaline, serrate to serrulate, the apex shortly acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with idioblasts and usually conspicuous stomata throughout, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, frequently with obscure idioblasts and stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis, without an adaxial flap, lance-ovate to ovate,  $1-1.7 \times 0.5-0.6$  mm, with a well-developed, denticulate keel along midrib, the base rounded, the margins hyaline, serrulate, the apex shortly aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present only on the lower surface. Megasporangia in two ventral rows or frequently absent; megaspores snow-, bone-white, or cream, with an equatorial flange, the proximal face rugose-granulate to granulate-reticulate with open reticulum of rather high ridges, the distal face reticulate with open reticulum of low to moderately high ridges,  $230-240 \mu\text{m}$  diam. Microsporangia in two dorsal rows, frequently on the apical region of ventral side of strobili, or strobili wholly microsporangiate; microspores tan, with a weakly developed equatorial flange, the proximal face slightly rugose to smooth, the distal face baculate to clavate,  $20-23 \mu\text{m}$  diam.

**HABITAT AND DISTRIBUTION:** In lowland to montane forest, on open to

shady roadside or stream banks, or forested slopes; 0-1800 m; Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Martinique?, Colombia, Venezuela, Trinidad, Tobago, Guyana, Surinam, French Guiana, Ecuador, Peru, Bolivia, and Brazil.

COMMON NAME: Cayapa: "Chigaso tape" [Ecuador, Kvist 40505, AAU, QCA]; Huambisa Jívaro: "juu" [Peru, Lewis et al. 12945, MO].

USE: The leaves are macerated and used for incised wounds to stop bleedings [Ecuador, Kvist 40505, AAU, QCA]; poultice of plant applied to cuts [Peru, Lewis et al. 12945, MO].

SPECIMENS EXAMINED: MEXICO. CHIAPAS: Cacahoatán, 1-2 km S of Cacahoatán, 450 m, 15 Jan 1973, Breedlove & A. R. Smith 31585 (DS); Cacahoatán, 550 m, 9 Aug 1935, Fisher 35398 (US); La Concordia, 96 km S of Mexican Highway 190 on road to Nuevo Concordia, 750 m, 10 Oct 1974, Breedlove 38478 (DS); Frontera Comalapa, 6-8 km E of Frontera Comalapa along road to Ciudad Cuauhtemoc, 1000 m, 23 Oct 1974, Breedlove 39135 (DS); Ocosingo, ruins of Yaxchilán, Río Usumacinta, 300 m, 26 Feb 1973, Breedlove 33958 (DS); Ocosingo, 3 km al NW del vértice del Chixoy, camino a Boca Lacatum, 120 m, 11 Sep 1985, E. Martínez 13643 (ENCB, MO); Tonalá, NW side of Cerro Vernal, 25-30 km SE of Tonalá, 400-600 m, 23 Jun 1972, Breedlove 25606 (DS), Cerro Vernal, 21 km S of Tonalá, 750 m, 5 Oct 1974, Breedlove

38104 (DS); Villa Corzo, 58 km S of Mexican Highway 190 on road to Nueva Concordia, 900 m, 11 Sep 1974, Breedlove 37635B (DS p.p.), 65 km S of Mexican Highway 190 on road from Tuxtla Gutiérrez to Nueva Concordia, 850 m, 12 Sep 1974, Breedlove 37686 (DS), 37789 (DS, ENCB), Río San Pedro, 86 km S of Mexican Highway 190 on road to Nueva Concordia near El Brillante, 650 m, 9 Oct 1974, Breedlove 38422 (DS); G. Münch 192 (DS). COLIMA: Nevado de Colima, Gadow & Gadow (BM). OAXACA: Juchitán, Isthmus of Tehuantepec, 11 km N of Matías Romero, 700 ft [213 m], 19 Oct 1969, Mickel 4193 (NY-2 sheets, UC), 4194 (NY, UC); Pochutla, 13 km N of Pochutla, Puente Azufre, 800 ft [244 m], 30 Sep 1970, Mickel 5133A (NY, UC), 18 km N of Pochutla, Mickel 5145 (NY, UC).

GUATEMALA. ALTA VERAPAZ: Cubilquitz, 350 m, Aug 1903, von Türckheim 8653 (K, M, US); Finca Mocca, 3200 ft [976 m], 7 Dec 1919, H. Johson 97 (US). PETÉN: Along Río San Román, W of Chinajá, 30 Mar 1942, Steyermark 45512 (US). RETALHULEU: Vicinity of Retalhuleu, 240 m, 17 Feb - 1 Mar 1941, Standley 88639 (US), 88702 (US); banks of Río Xibana, Finca San José Nil, 25 Aug 1936, Hatch & Wilson 402 (US). SUCHITEPÉQUEZ: Mazatenango, Sep 1867, Bernoulli 472 (BR, NY). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Motagua, Aug 1870, Bernoulli & Cario 168 (P).

HONDURAS. CORTÉS: Pulhapanzak water fall of Río Lindo, 500 m, 12 Dec 1982, Molina et al. 31956 (F, MO). OLANCHO: Vicinity of Catacamas, 450-500 m, 18-26 Mar 1949, Standley 18443 (F); Catacamas, 19 Oct 1969, Barkley &

Hourcade 39620 (GH).

NICARAGUA. CHONTALES: Along road from Juigalpa NE toward La Libertad, ca. 17.4 km NE of Río Mayales, at ford of Río El Bízcocho, ca. 12°12'N, 85°17'W, 350-400 m, 23-25 Sep 1977, Stevens 4098 (NY, UC). ZELAYA: Bluefields, 1 Aug 1922, Danneberger (US). WITHOUT SPECIFIC PROVINCE: Segovia District, Sangsangta, 1926, Schramm 18 (US).

COSTA RICA. ALAJUELA: Camino San Ramón de San Mateo, Oct 1912, Brenes (NY); Carrillo de Poás, 23 Aug 1936, Quirós 555 (F); Pasoagres, 20 Nov 1923, Lankester 603A (BM). CARTAGO: near Turrialba, slope of Río Reventazón behind the Instituto Interamericano de Ciencias Agrícolas, ca. 600 m, 20 Aug 1967, Mickel 3335 (NY). GUANACASTE: Comelco property near Bagaces, area E, transect R2, 50 m, 29 Jun 1971, Opler 285 (F). HEREDIA: Braulio Carrillo Nat. Park, 400 m, Mar 1985, Barcock A89 (K); La Selva, Braulio Carrillo Nat. Park, 35 m, Mar 1985, Barcock A90 (K); Finca La Selva, OTS Field Station, 100 m, 17 May 1980, Grayum 2823 (MO); Finca La Selva, Puerto Viejo, 100 m, 18-19 Jun 1967, Hauke 463 (NY); upstream from Puerto Viejo, ca. 4 km at Finca La Selva, 125 m, 16 Aug 1967, Mickel 3546 (NY, US); La Selva Field Station, 2 mi upstream from Puerto Viejo, along Río Puerto Viejo, 28 Jun 1977, Pflughaupt 35 (F). PUNTARENAS: Near Aguabuena, Rincón de Osa, 20 m, 16 May 1971, Burch 4456 (NY); Río Agua Buena near airport to ca. 4 km above it, Rincón de Osa, Liesner 1990 (MO, US); slopes adjacent to airport, Rincón de Osa, 20-300 m, 8 Feb 1974, Liesner 1871B (F); Osa, along trail from Palmar Norte to Jalisco, on divide

between Quebrada Batambal and Quebrada Benjamín, SW slope of Fila Retinto, 8°58.5'N, 83°28'W, 300-400 m, 9 Dec 1988, Grayum et al. 9163 (MO, UC), 160 m, 14 Dec 1989, Grayum & Hammel 9544 (MO, UC); Osa Peninsula, Tropical Science Center Field Station by Ricón Airport, ca. 50 m, 11 Nov 1966, Hauke 291 (NY); Osa Peninsula, Tropical Science Center Field Station SW of Ricón de Osa, ca. 50 m, 16 Jul 1967, Mickel 2831 (NY); San Vito, Coto Brus, 1000-1100 m, w.d., Gómez 22928 (MO). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Capelladas, 1906, Alfaro 17178bis (P); Chirripo, Sep 1901, Tonduz 14552bis (MICH, P); forêts de Nicoya, Dec 1899, Tonduz 13761 (BM, P).

PANAMA. BOCAS DEL TORO: Chiriquicito to 5 mi S along Río Guarumo, 5-7 June 1967, Lewis et al. 2041 (MO). CHIRIQUÍ: Trail from San Félix to Cerro Flor, 300-2500 ft [91-762 m], 13 Aug 1939, Allen 1961 (BM, MO, US); Hart 22a (K). CANAL AREA: Ancón Hill, Nov-Dec 1923, Standley 25171A (BM); Barro Colorado Island, Barbour-Lathrop trail, 6 Dec 1967, Croat 4098 (MO); Barro Colorado Island, Barbour trail, 26 Sep 1968, Croat 6467 (MO); Barro Colorado Island, Barbour trail, 200-300 m, 23 Nov 1948, Killip 39970 (US); Quebrada Bonita, 70-80 m, 20 Dec 1934, Dodge & Allen s.n. (MO, NY), headwaters of Río Casaya, 6 km E of Gamboa, 27 Dec 1973, Nee 9018 (UC, US); near Corozal road, near Panamá, 13 Dec 1923, Standley 26850 (DS, U, US); Gamboa, 26 Dec 1923, Standley 28424 (BM); Madden Dam, 9°13'N, 79°37'W, 50 m, 6 Nov 1983, H. Churchill 3850 (UC); E of Summit Garden, in Madden Forest Preserve, Pacific water shed, near continental divide, 300 ft [91 m], 10 Aug 1961, Welch 19630

(NY); Madden Forest Preserve, across road from George W. Green Park, 300 ft [91 m], 20 Aug 1961, Welch 19859 (NY); Madden Forest, headwaters of Pedro Miguel River, across road from George W. Green, 20 Aug 1961, Welch 19986 (NY); Valley of Río Masambí, on the road to Las Cascadas Plantation, 20-100 m, 6 Feb 1911, Maxon 4676 (US); Pipeline road, 16.8 km from beginning of road, 0-100 m, 7 Sep 1974, Mori & Kallunki 1761 (MO); Fort San Lorenzo, Fort Sherman, 14 Jun 1923, Maxon & Valentine 7006 (US). COLÓN: hills near Río Boquerón, 150 m, 4 Sep 1977, Maas et al. 2841 (NY, U, Z). DARIÉN: Río Aruza, 24 Oct 1967, Bristan 1338 (NY); ca. 3 mi SSE of Pijibasal, ca. 9 mi S of El Real, vicinity of confluence of Dos Bocas and Río Pirre, 16 Dec 1980, Hartman 11994 (MO). PANAMÁ: Alajuela, 4 Nov 1917, Killip 2671 (US); Juan Díaz, 13 Jan 1918, Killip 2784 (US); Perlas Archipelago, San José Island (ca. 55 mi SSE of Balboa), 31 Oct 1944, Johnston 344 (BM, U), 2 Nov 1944, 366 (BM, U); 7 Jan 1946, 1049 (BM, US). VERAGUAS: Isla de Coiba, near María River, across bay from Colonia Penal, 200 ft [61 m], 22 Oct 1979, Antonio 2329 (UC); W of Soná, 500 m, 24 Nov 1938, Allen 1074a (BM).

MARTINIQUE?. without coll. data, May [18]96, without collector, 192 (US).

COLOMBIA. ANTIOQUIA: Anorí, Providencia, 200 m, 19 Apr 1977, Santa et al. 149 (COL, NY); Dabeiba, Quebrada Vallesí, 270 m, 10 Jul 1983, Santa & Brand 795 (COL, HUA), Río Chever, 350 m, 10 Jul 1983, Santa & Brand 799 (COL); carretera al mar, La Llorona, 400 m, 9 Jul 1983, Santa & Brand 782

(AAU, COL); Mutatá, Quebrada Longaní, 130 m, 12 Jul 1983, Santa & Brand 810 (HUA); Nariño, alrededor de los baños termales, 3 Dec 1976, Santa et al. 68 (COL, NY-2 sheets); San Luis, orilla del Río Dormilón, 1000-1200 m, 8 Oct 1978, Santa 395 (COL, NY-2 sheets); San Luis, 10 km S de las partidas a San Luis, sobre la vía Medellín-Bogotá, carretera Quebradas-Naranjales y La Cristalina, 5°55'N, 74°50'W, 24 Jun 1987, Callejas et al. 4168 (COL, NY); Segovia, Río Pocuné, carretera a Zaragoza, 900 m, 27 Apr 1983, Santa 583 (COL); Tarazá, Puerto Bélgica, 90 m, 5 May 1983, Santa 618 (COL, HUA); Turbo, Altos de Mulatos, 400 m, 13 Jul 1983, Santa & Barnd 839 (COL); Valdivia, bajando a Puerto Valdivia, 570 m, 5 May 1983, Santa 611 (COL); Valdivia, bajando a Puerto Valdivia, 500 m, 5 May 1983, Santa 613 (COL, HUA). **BOYACÁ:** Carretera Pajarito-Agua Azul, 400 m, 17 Oct 1967, Hagemann 739 (COL); Cordillera Oriental, vertiente Oriental, carretera entre Pajarito y Agua Azul, 650 m, 21 Oct 1967, R. Jaramillo & Murillo 3950 (COL). **CAQUETÁ:** Florencia, carretera Florencia-Neiva, Quebrada La Unión, 460 m, 25 Jun 1987, Santa 1250 (AAU, HUA); Solano, 8 km SE of Tres Esquinas, on Río Caquetá below mouth of Río Ortegua, walk 5 km SE of Solano, 200 m, 5 Mar 1945, E. Little & R. Little 9583 (COL). **CHOCÓ:** Acandí, San Francisco (Bahía Triganá), vereda Coquitall, cerca de Triganá, ca. 8°21'N, 77°09'W, 50-200 m, 2-4 Apr 1990, A. Arbeláez & S. Churchill 440 (NY). **CUNDINAMARCA:** Carretera Medina, Río Humea, 500-550 m, Murillo & Harker 2194 (NY). **MAGDALENA:** Sierra Nevada de Santa Marta, transecto Buritaca, Alto Río Buritaca, 1100 m, 4 Sep 1977, R. Jaramillo et al. 5592-B



(COL); near Onaca, 2500 ft [762 m], 15 Aug 1898-1901, H. H. Smith 2245 (BM, BR, G, GH, K, L, MICH, MO, NY-2 sheets, P, S-3 sheets, U, UC). META: Río Guatriquia, near Villavicencio, 500 m, 18 Mar 1939, Alston 7603 (BM); La Macarena, 1 hr sobre el Río Guayabero en la desembocadura del Río Losada, 2°20'N, 74°06'W, 410 m, 11 Aug 1988, Callejas & Marulanda 7073 (MO); Cordillera La Macarena, trocha entre el Río Güejar y el caño Guapayita, Guapayita, 500-600 m, 20-28 Dec 1950, Idrobo & Schultes 833 (BM p.p.), 600 m, Dec-Jan 1950-1951, Schultes 11172 (COL); San Juan de Arama, estación de Los Micos, desembocadura de Quebrada Honda en el Río Güejar, 26 Feb 1969, Pinto & Sastre 1094 (COL). NARIÑO: Piedrancha, Chucunés, 2-5 km Chucunés-La Planada, 1°06'N, 77°54'W, 1450 m, 19 May 1991, S. Churchill et al. 18285 (NY). QUINDIO: Salento, caserío Boquía, Quebrada Santa Rita, 1800 m, 11 Jun 1983, Santa & Hoyos 704 (COL), 705 (COL, HUA). SANTANDER: Magdalena Valley, between Sogamoso and Carare Rivers, vicinity of Barranca Bermeja, Puerto Parra, 100-500 m, 31 Jul 1936, Haught 1970 (US); Magdalena Valley, between Sogamoso and Carare Rivers, vicinity of Barranca Bermeja, ca. 100, 31 Jul 1936, Haught 1979 (GH, MICH, S, UC, US). VALLE: banks of Río Engaño, Digua Valley, 700 m, 4 Apr 1939, Alston 7878 (BM); Cordillera Occidental, cerca de Lituania, 1970 m, 4 Apr 1972, Cleef 2718 p.p. (US).

VENEZUELA. APURE: Paéz, campamento de Corpo Andes, along Río Arauca at Colombian border, roadside between Campamento Corpo Andes and El Nula, 30 Jun 1983, van der Werff & González 4654 (MO, UC); Paéz, Parcela

#3, ca. 25 km E of El Nula, 4 Jul 1983, van der Werff & González 4841 (MO).

**ARAGUA:** Guamitas, Parque Nacional, 760 m, 2 Dec 1938, Ll. Williams & Alston 205 (AAU, BM, MG, US); Guamitas, Parque Nacional, 29 Dec 38, Alston 5761 (BM); Mountains N of Maracay, 900 m, 7 Dec 1947, Box 3922 (BM); Maracay, Vogl (M). **BARINAS:** Pedraza, above El Algarrobo, 8°31'N, 70°35'W, 400 m, 3 Aug 1983, van der Werff & R. Ortiz 5844 (MO). **CARABOBO:** Between Carabobo and Tinaquillo, 500 m, 28 Dec 1938, Alston 5747 (BM); above Hacienda Cura, between Valencia and Maracay, 1000 m, 13 Jan 1939, Alston 6291 (B.M). **LARA:** Jiménez, Parque Nacional Yacambú, Quebrada Negra, from the base of the tunnel to the junction with Río Yacambú, 9°41'N, 69°30-31'W, 620-740 m, 24 Oct 1982, Davidse & González 20993 (MO, UC); Jimenéz, Paso de Angostura, represa de Yacambú, confluencia de Quebrada Honda con el Río Yacambú, 33 km SE of Sanare, 9°41'N, 69°31'W, 500 m, 28-31 Jul 1973, Steyermark & Espinoza 107607 (F, US). **MÉRIDA:** Santa Cruz de Zamora, 1000 m, 12 Feb 1939, Alston 6992 (AAU, BM, NY-2 sheets, QCA, US). **MIRANDA:** Cerros del Bachiller, margins of Quebrada Corozal, S of Santa Cruz, 10°09'N, 65°48'N, 20-65 m, 16-17 Mar 1978, Steyermark & Davidse 116301 (MO, UC). **PORTUGUESA:** Guanare, entre Boquemonte y Río Las Marías, 350 m, 27 Sep 1981, Ortega & Stergios 1283 (UC); Guanare, near Desembocadero, 9°10'N, 69°53'W, ca. 400 m, 2 Nov 1982, A. R. Smith et al. 857 (UC p.p.); Guanare, along road to San José de La Montaña, ca. 9°20'N, 69°43'W, ca. 500 m, 8 Nov 1982, A. R. Smith 1063 (MO, UC); Río María, NE de Boca de Monte, 28-32 km al NNE de Guanare, 9°18-19'N, 69°42-43'W,

400-500 m, 2 Nov 1982, Steyermark et al. 127086 (MO, UC); Guanare, 17 km NW of Tucupido, N slope of Fila Las Palmas, 9°01'N, 69°57'W, 200-400 m, 30 Oct 1982, Davidse et al. 21457 (MO); Ospino, Quebrada Honda, caserio La Cristobera, 18 Jul 1987, Ortega et al. 3090 (BM). SUCRE: Paria Peninsula, Cariaquita, 10-13 Mar 1911, Bond et al. 253 (US); Sucre, Quebrada Zurita, Paso Hondo, S de Limonal y Santa Fé, 40 m, 18 Aug 1973, Steyermark et al. 107820 (NY). TÁCHIRA: Córdoba, Cerro La Camiri, S of town of Río Negro, 7°36'N, 72°10'W, 430-530 m, 6 Nov 1982, Davidse & González 21554 (MO, UC); Río Frio, between junction of Río Quinimari and Río Frio, 8 km upstream to La Laguna, between pueblo of Río Negro and La Laguna, 7°35-36'N, 72°09-13'W, 480-500 m, 30 Jul 1979, Steyermark & Liesner 119091 (MO, UC). YARACUY: Hacienda Iboa, near Guama, Yaracuy, 400-500 m, 12 Sep 1923, Pittier 11145 (GH, NY, US); along gravel road 5.2 km E from plaza in Salom (W of Valencia, NE of Nirgua) which intersects Hwy connecting Montalban and Miranda, 10°10'N, 68°25'W, 780-790 m, 4 Aug 1982, Croat 54596 (MO, UC). ZULIA: Colón, 3 km E of the Río de Oro, settlement on the Río de Oro, ca. 9°18'N, 72°28'W, 100-250 m, 28 Jun 1980, Davidse et al. 18786 (MO, UC); Lagunillas, cuenca del Embalse Burro Negro (Pueblo Viejo), laderas occidentales de la Serranía de Ziruma o El Empalado, 13 Km N de Embalse, ca. 10°25'N, 70°49'W, 550-600 m, 1-5 Apr 1982, Bunting et al. 11288 (UC); Mara, cuenca del Río Guasare, alrededores del destacamento Guasare No. 1 (La Yolanda), 10°52'10"N, 72°29'30"W, 300-500 m, 16 Nov 1982, Bunting et al. 12394 (NY, UC); Mara, along Río Socuy (NW side), W of Cerro

Caracara, 5 km SW of Corpozulia Campamento Socuy, 10°54'N, 72°20'W, 80-90 m, 2 Jun 1980, Steyermark et al. 123131 (MO, UC); a lo largo de Quebrada Perayra, afluente del Río Tokuku (Tocucu), SE de la Misión de Los Angeles de Tokuku, SW de Machiques, 450-475 m, 29 Aug 1967, Steyermark 99844 (NY).  
**WITHOUT SPECIFIC STATE OR LOCALITY:** Alto Orinoco, Raudal de los Guaharibos, 27 Jul 1951, Croizat 383 (MO, NY).

TRINIDAD. Aripo, Hart 6318 (K); Big River bridge, Mason Hall, 13 Sep 1909, Broadway 3036 (BM, NY, S-2 sheets, U); Blanchisseuse road, 10,5 mi post, 16 Sep 1927, Broadway 6769 (K); Arouca, 7 Aug 1919, Broadway 15 (DS, NY); Blue Basin, 17 Apr 1920, E. Britton et al. 1909 (NY); Blue Basin, 8 Sep 1901, Went 1024 (U); near Blue Basin, Diego Martin, 1 Jan 1926, Broadway (K-2 sheets); botton of hill to Blue Basin, Diego Martin, 1 Jan 1926, Broadway 5871 (BM, BR, G, K, S); Ciparo, 1919, Broadway (DS p.p.); Diego Martin, 1919, Broadway (BM, DS, GH, K, NY); Blue Basin, near Port-of-Spain, 23 Aug 1939, Friend 123 (NY); Maracas, 14 Sep 1927, Broadway 6747 (BM, K, S, US); Maracas, 14 Oct 1927, Broadway 6700 (BM, K, S); Maracas, Hart 6322 (K, NY-2 sheets); Maracas Falls, 4 Aug 1937, Sandwith 953 (BM, K); Maracas Fall, 12 Sep 1901, Went 1054 (U); Maraval, 9 Dec 1928, Broadway 7045 (BM); Ortinola Estate, 4 Mar 1920, E. Britton & Coker 242 (NY, US); Pitty-valley, 25 Oct 1950, J. Florschütz 71 (BM, U); St. Ann, 17 Mar 1920, N. Britton et al. 664 (NY); St. Ann's Cascade, 12 Nov 1923, Broadway 5069 (NY p.p.); St. Ann, Chancellor road, 12 Oct 1929, Broadway 7426 (BM p.p., F); St. Ann, 17 Oct 1931, Broadway 7894

(BM, S, Z); Santa Cruz, 8 Jul 1927, Broadway 6657 (K); Santa Cruz Mountains, 23 Dec 1907, Broadway 7030 (K); Santa Cruz, 23 Aug 1931, Broadway 7719 (BM, S). WITHOUT SPECIFIC LOCALITY: Bernard Estate, Jul 1908, Broadway (NY); 1931, Homersley (BM); Jenman 6314 (K, NY), 6322 (NY); 500 ft [152 m], 1932, Rodger 10 (BM); Apr 1886, Sherring (NY).

TOBAGO. Bacolet River, 31 Oct 1889, Eggers 5697 (P-2 sheets, S p.p.); Franklin, 30 Jul 1909, Broadway 2928 (US); Frenchfields, 800 ft [244 m], Oct 1889, Eggers 5584 (L, O, P-3 sheets, US); Le Coteaux, 9 Nov 1932, Broadway 9094 (BM); Oct 9, Sandwith 1684 (K).

GUYANA. [BERBICE]: Sierra Acarai Region, near the Guyana-Brazil boundary, 100 yards from New River, 0.25 mi S of Camp 3 (ca. 5 mi S of the upper reaches of the Mataruki River, which is tributary of the Essequibo, 1°35'N, 58°30'W, 5 Oct 1952, Guppy 378 (BM).

SURINAM. Bofroe-holo, Tangimamma, Boven-Coppename, 19 Nov 1954, Mennega 473 (U); Brokopondo, 1 km ten Z. van de proeftuin, 13 Dec 1963, van Doesburg 208 (U); Z-helling Julianatop, 550 m, 1 Aug 1963, Schulz 10270 (U); S vicinity of Kappelsavanna near the S foot of Tafelberg, 13 Jun 1963, Wessel-Boer 1570 (U); Nassau, S of Km 7, 12 Mar 1949, Lanjouw & Lindeman 2625 (U), 24 Mar 1949, 2898 (U); confluence of Paloemeu and Tapanahoni rivers, 12 km upstream on the Paloemeu River, 3°20'N, 55°27'W, 16 Apr 1963, Wessels-Boer 1315 (BM, U); Prinses Irene-vallen bij Brownsberg, Feb 1959, Lanjouw (U); Mt. Stoffoekoe (Saramacca R.), Aug 1957, Schulz 8054 (U); Wonotobo falls, 5 Aug

1935, Rombouts 81 (U). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Dumortier (U).

FRENCH GUIANA. Fleuve Approuague, Rivière Arataye, Saut Pararé, 1 Sep 1977, Sastre 5861 (BM); Vallée de la Haute Approuague, Massif des Emerillons, 15 Dec 1983, Feuillet 1244 (BM, Z), 16 Dec 1983, Feuillet 1292 (BM, Z p.p.); Massif des Emerillons, centre nord sources de l'Approuague, 250 m, 18 Sep 1980, Cremers 6711 (Z); Inini R., Monts Inini, 3°28'N, 52°36'30"W, 7 Aug 1985, Cremers et al. 8756 (BM, NY, U, Z); Montagne de l'Inini, zone centrale, extrémité NW, 350 m, 3°31'N, 53°35'W, 11 Sep 1985, Cremers et al. 9303 (U); Station des Nouragues, bassin de l'Approuague, Arataye Chemin Coco, 4°03'S, 52°42'W, 125 m, 17 Nov 1989, Cremers 10824 (BM, US, Z); Riv. Mana, Gros Saut, 25 Jul 1981, Cremers 7309 (Z); Oyapock, May 1908, Blanc (S); Haut Oyapock, les Trois Sauts, 21 May 1970, Oldeman B-3313 (P, U, US); Rio Oiapoque [Oyapok], near Cachoeira Tres Saltos [Trois Sauts], 2°12'N, 52°53'W, 10 Sep 1960, Irwin et al. 48149 (MG, NY, U, US); 13 km SSW du village de Saül et a 2-3 km W of the crique Limonade, 31 Mar 1983, Granville 5438 (BM, Z); embouchure du Yaroupi, affluent de l'Oyapock, Oldeman B-3184 (BM).

ECUADOR. ESMERALDAS: Río Cayapa, Río Zapallo Grande, 0°47'N, 78°53'W, 100 m, 2 Jul 1982, Kvist 40505 (AAU, QCA). MORONA-SANTIAGO: Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner," km 140 on road Loja-Gualaquiza, 3°37'S, 78°34'W, 900-1000 m, 26-27 Apr 1973, Holm-Nielsen et al. 4627 (MO, S). NAPO: Añangu, Río Napo, 0°31'-32'S, 76°23'W, 260-350 m, 1 May

1983, Lawesson et al. 39556 (AAU); road Baeza-Lago Agrio, 0°08'S, 77°36'W, 1400 m, 7 Aug 1980, Øllgaard et al. 35702 (AAU), 35712 (AAU, MO); Río Cuyabeno, 0°06'S, 76°10'W, 300 m, 20 Aug 1981, Brandbyge et al. 33827 (AAU); Río Eno near San Pablo at Río Aguarico, 0°11'S, 76°31'W, 250 m, 20 Feb 1984, Lægaard 51530 (AAU, QCA); Hollín-Loreto road, 17 km La Cascada Río Hollín, 0°40'S, 77°45'W, 1200 m, 24 Jan 1991, Moran & Rohrbach 5110 (MO, UC); San Pablo de Secoyas, 0°15'S, 76°21'W, 4 Aug 1981, Brandbyge et al. 32992 (AAU). **PASTAZA:** Mera-Shell Mera, ca. 2 km E of Mera, at bridge over Río Alpayacu, 1°28'S, 78°6'W, 1100 m, 21 Jan 1992, Øllgaard 99567 (AAU). **PICHINCHA:** Quito-Mindo road, 5000 ft [1525 m], 17 May 1958, Prescott 1453 (NY); Quito-Mindo road, 5000-6000 ft [1525-1830 m], 18 May 1958, Prescott 1460 (NY); Santo Domingo de Los Colorados, Aug 1875, Sodiro (K). **WITHOUT SPECIFIC PROVINCE OR LOCALITY:** Vicinity of Quininde, 50-150 m, 8-13 Apr 1943, Holdridge 1665 (GH, NY, US); 1882, Sodiro (K).

**PERU.** Cuzco: La Convención, Río Manguriari, Alto Urubamba, upstream to Río Maguriari, 12°47'S, 72°40'W, 750 m, 2 Feb 1991, Núñez & G. Ortiz 12741 (UC). **HUÁNUCO:** Huánuco, Cueva de Las Pavas, near Tingo María, 500-600 m, 2 Feb 1948, Ferreyra 2892 (BM p.p.); Leoncio Prado, Rupa Rupa, Cueva Las Pavas, 5 km S de Tingo María, 672 m, 4 Jul 1969, J. Schunke 3257 (NY). **JUNÍN:** Chanchamayo Valley, C. Schunke 189 (BM); La Merced, 700 m, 29 May-4 Jun 1929, Killip & A. C. Smith 24021 (NY); E of Quimirí Bridge, near La Merced, 800-1300 m, 1-3 Jun 1929, Killip & A. C. Smith 23945 (NY, US). **LORETO:** Alto

Amazonas, Petro Estación Morona, Río Morona, 4°20'S, 77°20'W, 160 m, 22 Mar 1987, Lewis et al. 12945 (MO); Coronel Portillo, Padre Abad, Boquerón de Padre Abad, 400 m, 19 May 1969, J. Schunke 3066 (NY p.p.); between Yurimaguas and Balsapuerto (lower Río Huallaga basin), 135-150 m, 26-31 Aug 1929, Killip & A. C. Smith 28350 (BM, NY); above Pongo de Manseriche, 220 m, 3 Jan 1932, Mexia 6366a (BM). MADRE DE DIOS: Madre de Dios, Oct 1893, Jay a (NY). PASCO: Oxapampa, trail between Yanahuanca and Chumalli along Río Pozuzo, 820-1100 m, 15-16 Mar 1984, D. Smith et al. 6382 (UC). SAN MARTÍN: Juan Jui, Alto Río Huallaga, 400-800 m, Jan 1936, Klug 4230 (BM, K, MO, NY, S, U). WITHOUT SPECIFIC DEPARTMENT OR LOCALITY: Pöppig 184 (G).

BOLIVIA. SANTA CRUZ: Ichilo, Parque Nacional Amboro, along Río Saguayo, 17°40'S, 63°43'30"W, 450 m, 22 Sep 1990, Nee 38868 (MO, NY). WITHOUT SPECIFIC PROVINCE OR LOCALITY: Antahuacana, quebrada del Río Espíritu Santo, 750 m, Jun 1909, Buchtien 2252 (BM-2 sheets, M, P, S-3 sheets, UC, US); Cordillera Real, Guanay, 1800 ft [549 m], 14-16 Apr 1926, Tate 557 (NY-2 sheets).

BRAZIL. AMAPÁ: W bank of Rio Falsino, ca. 10 km upstream from confluence with Rio Araguari and ca. 8 hrs by boat from Pôrto Grande, 1°00'N, 51°40'W, 28 Sep 1987, Pruski et al. 3292 (NY, UC); Rio Oyapock, Rio Gauropi, Jul 1927, Luetzelburg 20284 (M). AMAZONAS: Bocca do Tejo, Rio Juruá, May 1901, Ule 5524 (G, K, L, P). GOIÁS: Presidente Kennedy, road from highway BR-153 to Itaporã, 12 km W of village of Presidente Kennedy, Fazenda Primavera



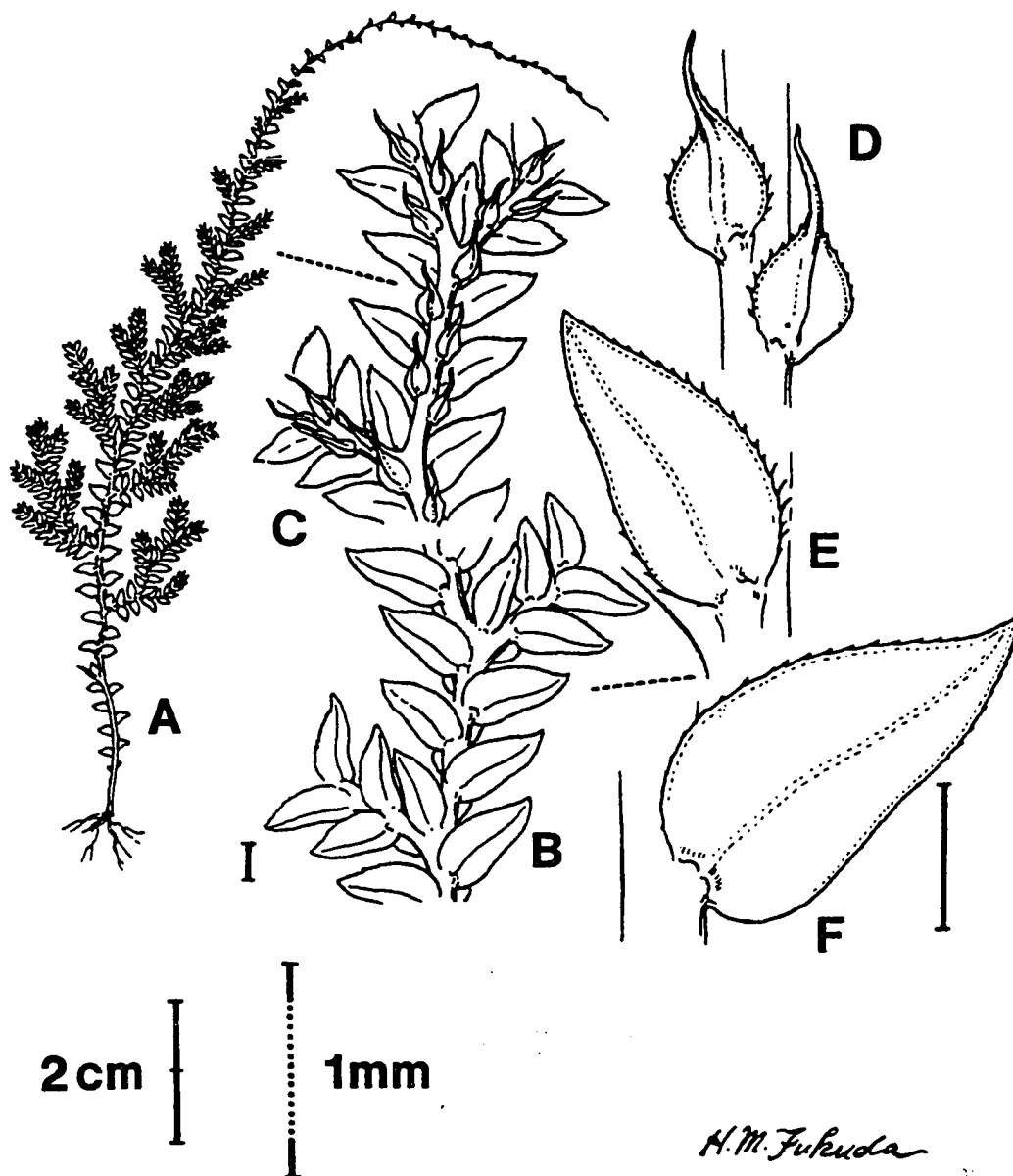
along Ribeirão Feíinho, ca. 3°25'S, 48°37'W, 400-500 m, 4 Feb 1980, Plowman et al. 8436 (MICH, NY, US). MATO GROSSO: Poaia, Buritizinho, 17 Apr 1894, Lindman A3265 (G, GH, NY, S-2 sheets). PARÁ: Serra dos Carajás, AMZA camp N-5, 6°04'S, 50°08'W, 700-750 m, 12 May 1982, Sperling et al. 5589 (NY); Conceição, near Córrego São João and Troncamento Santa Teresa, ca. 8°03'S, 50°10'W, 350-620 m, 9 Feb 1980, Plowman et al. 8584 (MICH, NY, US); W bank of Rio Maicuru, ca. 23 km upstream from Lageira airstrip, 0°55'S, 54°26'W, 29 Jul 1981, Strudwick et al. 3696 (MO, NY-2 sheets), 3764 (NY), 3773 (NY), 3780 (NY). RONDÔNIA: 128 km SW of Ariqueaes at Mibrasa Mining Camp, 3k E of camp, 16-17 May 1982, McFarland et al. 199 (NY); 120 km SW of Porto Velho via highway BR-364, 20 km N of Mibrasa, Santa Barbara Mining Camp office, 9°10'S, 63°07'W, 25 May 1982, McFarland et al. 274 (NY); Porto Velho, ca. 5 km S of Campo Novo, on road to old mining area at Balateiro, 10°38'S, 63°37'W, 300 m, 23 Apr 1987, Nee 34989 (MICH, NY).

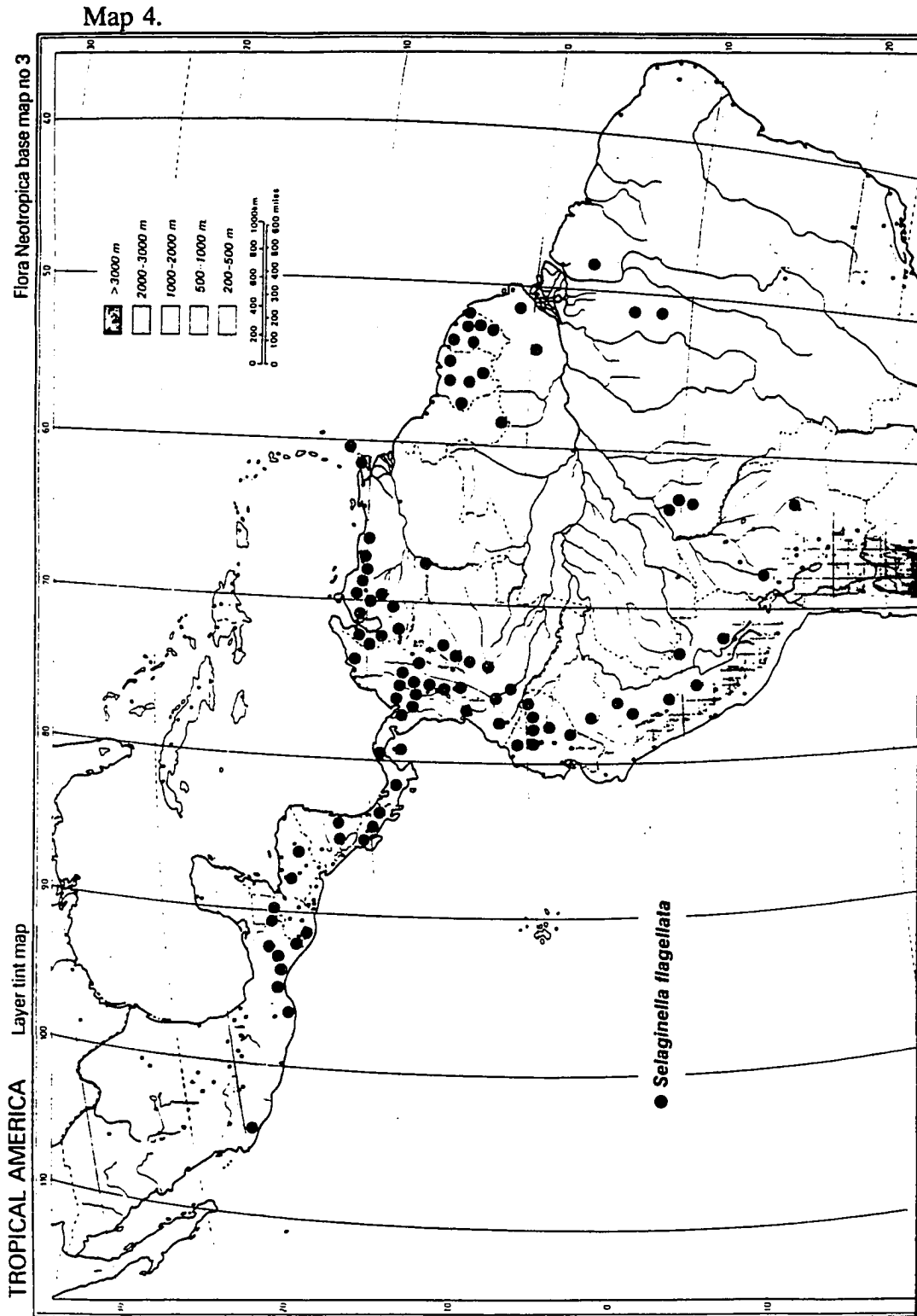
NOMENCLATURAL COMMENTS: There is a problem regarding the correct holotype of S. flagellata. Spring (1843) when describing S. flagellata cited only "Hab. in Guyana gallica (Leprieur)," without any indication as to where this collection was located. Later, Spring (1849) elaborated more on the type collection and cited "Hab. in Guyana gallica [rupes dense obtegens as rivulus Oyapok superioris, fr. Jun.: Leprieur (H.M.P., H. Deless.)." The modern abbreviations for these two herbaria are P and G, respectively. Some recent authors

(Alston et al., 1981; Lellinger, 1989; Mickel & Beitel, 1988; R. Tryon & Stolze, 1994) erroneously have considered that the holotype of S. flagellata was located at LG. This is incorrect for two reasons: 1) while it is true that Spring (1843) originally did not cite any herbaria, he later (Spring, 1849) cited only two herbaria (P and G) as having the type collection, never mentioning LG. In fact, Badré (1983) who listed Spring's types at LG did not include the type of S. flagellata among the types located there. Moreover, among the collections I received on loan from LG, I have not found the presumed holotype, and therefore it can be assumed that this collection is not there; 2) According to the current Code of Botanical Nomenclature (Greuter, 1994) since no holotype was originally indicated by Spring (1843), a lectotype may be designated. In accordance with recommendation 9A of the code, only the original material at P and G should be considered as possible lectotypes. They clearly indicate the intent by the author of the name, in this case Spring.

One of the syntypes of S. ambigua var. fallax, not listed above, (Fendler 108, B, BM, CAS, F, GH, K, MICH, NY, UC, US, YU), is actually S. tenella.

Fig. 19. A-F. Selaginella flagellata (Mickel 5133a, NY). A. Habit. B. Lower surface of branch. C. Upper surface of branch. D. Median leaves. E. Axillary leaf. F. Lateral leaf.





**28. *Selaginella stenophylla* A. Braun, Index Sem. Hort. Berol. App.: 22. 1857.**

Type: Cultivated material at Horto Botanico Berolinensi, 1857, Braun (Lectotype: B!, here designated; isoelectotypes: B-4 sheets!, M!). Probable isoelectotype: Cultivated material at Horto Botanico Berolinensi, Apr 1851 [1857?], Braun (US-2 sheets! [one a fragment]).

**Selaginella incurvata Baker, J. Bot. 21: 99. 1883.**

Type: MEXICO. VERACRUZ: Liebmann (Holotype: K-n.v.; isotype: fragment NY!).

**Selaginella miradorensis Hieronymus, Hedwigia 43: 30. 1904.**

Type: MEXICO. SAN LUIS POTOSÍ: Tamasopo Canyon, 1 Oct 1890, Pringle 3293 (Lectotype: B!, here designated; isoelectotypes: BM!, BR!, CAS!, DS-2 sheets!, K-2 sheets!, L-2 sheets!, M!, MICH-4 sheets!, NY-2 sheets!, P-2 sheets!, UC!, US!, W!). Other syntypes: MEXICO. VERACRUZ: Mirador, 1856, Sartorius 185 (B!); Mirador, May [1867?], Schaffner 6 (B-2 sheets!, K!, P!, W-2 sheets!), 6a (B!, W!); Valle Córdoba [Córdoba], 15 Dec 1865, (Bourgeau 1654 (B?-n.v., K!, P!, US!); Cuesta de Pinolco, Ehrenberg (B?-n.v.); prope urbem Orizaba, 1869, Weber (W!)).

Plants terrestrial or epipetric. Stems creeping, greenish or stramineous, to ca. 35 cm long, 0.5-1.4 mm diam., not articulate, not flagelliform, not stoloniferous, 3- or 4-branched. Rhizophores ventro-axillary, restricted to basal ½ or throughout the stem, stout, 0.5-0.8 mm diam. Leaves dimorphic throughout, chartaceous, the

upper surface green or brownish when old, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green or brownish when old, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to or strongly clasping the stem, oblong, oblong-lanceolate, or oblong-ovate,  $(1.5-2-3.7 \times (0.6-1-1.5 \text{ mm})$ ; the acroscopic base rounded to semicordate, strongly overlapping the stem, the basiscopic base rounded to geniculate, not overlapping the stem; margins hyaline, the acroscopic margin serrate along basal  $\frac{1}{2}$ , serrulate apically, the basiscopic margin entire to serrulate apically, without conspicuous stomata; apex broadly acute, obtuse, or rounded, dentate at tip; the upper surface glabrous, frequently with conspicuous or less frequently obscure idioblasts, without conspicuous stomata, the lower surface glabrous, with conspicuous idioblasts, and with stomata along midrib. Median leaves distant, ascending, elliptic or elliptic-ovate,  $1.3-2 \times 0.6-1.2 \text{ mm}$ ; base frequently with both an inner and an outer auricle distinctly free from the stem, or the inner auricle less developed and weakly distinct from the stem, the auricles ciliate-denticulate or long-ciliate; margins hyaline, long-ciliate along basal  $\frac{1}{2}$ , especially along the inner margin, short-ciliate to serrate apically; apex abruptly aristate, the arista  $\frac{1}{4}$  to  $\frac{1}{2}$  the length of the lamina, 0.3-0.8 mm long, puberulent, dentate at tip, both surfaces glabrous, the upper surface with conspicuous idioblasts, with stomata along midrib, the lower surface without idioblasts or stomata. Axillary leaves similar to lateral leaves or lanceolate to lance-ovate and subcordate. Strobili terminal on branch tips, lax and flattened, dorsiventral, 3-10

mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{1}{2}$  to  $\frac{3}{4}$  the sporophyll length, asymmetric or lanceolate,  $1.4-2.2 \times 0.5-0.8$  mm, with a well developed, denticulate keel along midrib, the base rounded, the margins narrowly hyaline, serrate to serrulate, the apex acute, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with idioblasts, with stomata along midrib, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, with or without obscure idioblasts or stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis, without an adaxial flap, ovate to ovate-lanceolate,  $1.3-1.8 \times 0.4-0.8$  mm, with a strongly developed, denticulate to entire keel along midrib, the base rounded, the margins narrowly hyaline, serrate to serrulate, the apex acute to short-acuminate, both surfaces composed of elongate cells with sinuate walls, glabrous, with obscure idioblasts, the stomata present only on the lower surface along the midrib. Megasporangia in two ventral rows; megaspores white, infrequently cream to brownish, with a prominent equatorial flange, the proximal face granular-striate, striate-reticulate, with close to open reticulum of low ridges, the distal face reticulate with open reticulum of high ridges,  $330-356 \mu\text{m}$  diam. Microsporangia in two dorsal rows; microspores not studied.

HABITAT AND DISTRIBUTION: In shaded, damp areas, on limestone slopes,



and on mossy rocks; 150-1300 m; Mexico and Guatemala.

SELECTED SPECIMENS EXAMINED: MEXICO. CHIAPAS: Estación Juárez, 10 km Teapa-Pichucalco, a 50 m de la carretera, 160 m, 13 Feb 1989, Ishiki et al. 2025 (NY). HIDALGO: S of Tamazunchale, San Luis Potosí, 1.8 mi S of Hidalgo-SLP border along highway 85, 13 Jan 1984, Lavin et al. 4635 (NY). PUEBLA: Huauchinango, Salto Grande, 1000 m, 10 Feb 1932, Fröderström & Hultén 750 (NY). QUERÉTARO: Landa, 10 km SE de Agua Zarca, 800 m, 31 Jul 1987, Rzedowski 43867 (NY). SAN LUIS POTOSÍ: Huichihuayón, 150 m, 6 Oct-3 Nov 1940, V. Grant 521 (MICH); Tamasopo Canyon, 1 Oct 1890, Pringle 3293 (B, BM, BR, CAS, DS-2 sheets, K-2 sheets, L-2 sheets, M!, MICH-4 sheets, NY-2 sheets, P-2 sheets, UC, US, W, lectotype coll. of S. miradorensis); Tamazunchale, alrededores de Tamán, 400 m, 28 Jun 1959, Rzedowski 11016 (NY). TAMAULIPAS: Gómez Farias, vicinity of Rancho del Cielo Biological Station, 5.5 km NW of Gómez Farias, 1100-1150 m, 19 Jun 1982, Nee & Diggs 24511 (NY). VERACRUZ: Chocamán, barranca between Coscomatepec and Chocamán along hwy. Mex 143, 9 km (by air) SSE of Coscomatepec, 19°02'N, 97°01'45"W, 1300 m, 12 Dec 1985, Nee & Andres 32104 (NY); Liebmann (fragment NY, type coll. of S. incurvata); Mirador, 1856, Sartorius 185 (B, syntype coll. of S. miradorensis); Mirador, May [1867?], Schaffner 6 (B-2 sheets, K, P, W-2 sheets, syntype coll. of S. miradorensis), 6a (B, W, syntype coll. of S. miradorensis); Valle Córdova [Córdoba], 15 Dec 1865, (Bourgeau 1654 (K, P, US, syntype coll. of S.

miradorensis); prope urbem Orizaba, 1869, Weber (W, syntype coll. of S. miradorensis).

GUATEMALA. ALTA VERAPAZ: Along road to San Pedro Carcha, ca. 3 km ENE of Cobán, 30 Jan 1977, King 7326a (UC, US); Cobán, 1350 m, Jul 1906, von Türkheim II1268 (BR, GH, P, W).

NOMENCLATURAL COMMENTS: A. Braun (1857) based the description of S. stenophylla on cultivated material at B without citing a specific collection. Among the specimens I have seen from B there are several presumed syntypes collected and annotated by Braun in 1857. Reed (1965-1966), listed as type of this species a specimen at US dated April 1851. Gregory and Riba (1979) cited as the type a specimen at B also dated 1851. Gregory and Riba (1979) have stated, however, that they did not examine any type material for their study and cited types only from the literature, in this case most probably from Reed's Index Selaginellarum. The handwritten label on the specimen at US was apparently made by Hieronymus and does not bear Braun's annotation. None of the specimens I received from B were labeled 1851. It is possible that Hieronymus misnumbered the label on the specimen sent to US and that instead of 1851 it should have been 1857. This may help explain why there is no specimen labeled 1851 among those seen from B. Moreover, there is no certainty that Braun ever saw the specimen now at US. On the other hand, the year found on labels of specimens at B correspond to the same year of the publication of S. stenophylla.

In selecting a lectotype for this species and in accordance with the ICBN (Greuter, 1994), it seems advisable to consider only those specimens at B, which were definitively seen by Braun when describing the species, as possible lectotypes.

TAXONOMIC DISCUSSION: The very long, creeping stems, the mostly oblong lateral leaves with broadly acute to rounded apices, the median leaves with a well developed outer auricle, and the stout rhizophores (0.5-0.8) distinguish S. stenophylla from all other species treated, except for S. karowtipuensis. In addition to the characters given in the key S. stenophylla differs from S. karowtipuensis in its geographic distribution. Selaginella stenophylla is found only in Mexico and Guatemala, whereas S. karowtipuensis is found only in Guiana.

**29. *Selaginella tenella* (P. Beauvois) Spring, Bull. Acad. Roy. Sci. Bruxelles 10:**

234. 1843. (Figs. 1C; 8A-O; 9A & B).

*Diplostachium tenellum* P. Beauvois, Mag. Encycl. 9<sup>e</sup> Année, 5: 481. 1804.

Neotype (chosen by Proctor, 1985): PUERTO RICO. *India occidentalis* in

Portorico ex Herb. Vent. [Ventenat] (P-herb Desv.-n.v., photo BM!).

*Lycopodium tenellum* (P. Beauvois) Desvaux ex Poiret, Encycl. Suppl. 3: 553.

1814.

Type: Same as above.

*Selaginella albo-nitens* Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 139. 1843.

Lectotype (chosen by Badré, 1983): GUADELOUPE. L'Herminier (LG!;

isolectotype: B!, probable isolectotype: BR!, YU!).

*Selaginella cladorrhizans* A. Braun, Ann. Sci. Nat. Bot. V, 3: 282. 1865.

Syntypes: VENEZUELA. ARAGUA: Colonia Tovar, Fendler 324 p.p. (B-n.v.,

BM!, E!, F!, G-2 sheets!, K!, NY!, US!, YU!); FALCÓN: San Carlos, Moritz

448 (B-n.v., BM!, K!).

*Selaginella mollis* Fée, Mém. Foug. 11: 133. 1866, non A. Braun (1865).

Type: GUADELOUPE. St. Louis, L'Herminier (B!, BM!, BR!, DS!, K!,

P?-n.v., W!).

*Selaginella subcaulescens* Baker, J. Bot. 22: 277. 1884.

Type: CUBA. Wright 1822 (Holotype: K!; isotypes: B!, BM!, G!, GH!,

MO!, NY!, P!, S!, YU!).

*Selaginella albonitens* forma typica Hieronymus, Hedwigia 58: 311. 1917, nom.

illeg., hence to be rej.

Selaginella albonitens forma longiciliata Hieronymus, Hedwigia 58: 313. 1917.

Syntypes: SANTO DOMINGO [REP. DOMINICANA]. Río Mameyas, 200 m, 19 Jun 1887, Eggers 2504b (B?-n.v.); Mt. Isabel de la Torre, 300 m, 10 Jun 1887, Eggers 2504c (B?-n.v.); Mt. Isabel de la Torre, 600 m, s.d., Eggers 2611b (B?-n.v., as 2611 K!, M!). PUERTO RICO. Near Cayey, Pedro Avila, 22 Sep 1885, Sintenis 1333b (B-2 sheets!); Near La Lima, 21 Oct 1885, Sintenis 2246b (B!); Near Yauco, Río Duey, Mt. Rodadero, 5 Feb 1886, Sintenis 3627 (B-2 sheets!); Road between Utuado and Arecibo, 13 Jul 1901, Underwood & Griggs 825 (B!, NY-2 sheets!, US!), 836 (B!, NY!); Without specific locality, 13 May 1906, Cowell 994 (B!, as Britton & Cowell 994 NY!).

Selaginella sintenisii Hieronymus, Hedwigia 58: 299. 1917.

Syntypes: CUBA. Oriente, near Villa Monte Verde, 1859, Wright 940 p.p. (B!, BM!, BR!, G!, GH-2 sheets!, K-4 sheets!, MO!, NY!, P!, S!, US!, YU!); Without data, 1865, Wright 7 (B!); Near Jagüey, 500 m, 25 Mar 1889, Eggers 4889 (B!, BM!, F!, K!, P!, US!); Oriente, Río Macaguanica, 17 Feb 1910, Shafer 3979 (A!, B!, NY!); Oriente, near Gran Piedra, 1500 m, 4-5 Mar 1911, Shafer 9001 (A!, B!, BM!, NY!, US!); Baracoa, near Cooper's Ranch, base of Mt. El Yunque, Mar 1903, Underwood & Earle 983 (B-2 sheets!, BM!, NY-2 sheets!); Oriente, Yateras, SE of Jagüey, Posesion de Starck, 450-525 m, 3 May 1907, Maxon 4440 (B!, B!, GH!,

NY!, US!). JAMAICA. Near Troy, Cockpit, 13-18 Sep 1906, Underwood 3320 (B!, NY!, US!). PUERTO RICO. Eneas, near Pepino, 10 Jan 1887, Sintenis 5837 p.p. (B!, K!, M!); Sintenis 5838 (B?-n.v., S!); Los Angeles near Utuado, 17 Jan 1887, Sintenis 5912 (B!, BM-n.v., NY!, US!); Sierra de Lares, Guajataca, 16 Feb 1887, Sintenis 6245 (A!, B!, G!, K!, M!, US!).

Plants terrestrial or epipetric. Stems ascending, suberect, or erect, stramineous, 3-15 cm long, 0.4-1 mm diam., not articulate, the stem apex infrequently flagelliform, stoloniferous, 2 or 3-branched, the branches frequently flagelliform. Rhizophores axillary, restricted to basal  $\frac{1}{4}$  or throughout the stem on flagelliform plants, filiform, 0.1-0.5 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, ovate, ovate-oblong, or oblong,  $1.2-3 \times 0.5-2.5$  mm; base rounded to subcordate, the acroscopic base strongly overlapping the stem, the basiscopic base rounded, not overlapping the stem; the acroscopic margin narrowly hyaline or pale green, short-ciliate near the base or serrate to serrulate throughout, the basiscopic margin narrowly hyaline or pale green, entire to serrulate; apex acute, dentate at tip; the upper surface glabrous, with idioblasts, the lower surface glabrous, usually with conspicuous or obscure idioblasts, and with stomata along midrib. Median leaves distant, ascending, broadly ovate, ovate-lanceolate, or ovate-elliptic, 0.7-2

× 0.4-1.4 mm; base asymmetric to oblique, entire; margins hyaline, serrate; apex acuminate, long-acuminate, or long-aristate, the acumen or arista  $\frac{1}{2}$  or less the length of the lamina, 0.2-0.7 mm long, frequently puberulent, dentate at tip, both surfaces glabrous, the upper surface with idioblasts, with stomata along midrib and frequently with scattered throughout the lamina, the lower surface without idioblasts and stomata. Axillary leaves similar to lateral leaves. Strobili terminal on branch tips and stem apex, lax and flattened, dorsiventral, 2-9 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending  $\frac{1}{4}$  to  $\frac{1}{2}$  sporophyll length, asymmetric or ovate to ovate-lanceolate, 1-2.5 × 0.4-0.9 mm, with a weakly to strongly developed, denticulate keel along apical  $\frac{1}{2}$  of midrib, the base rounded, the margins hyaline, serrate to serrulate, the apex acuminate to shortly aristate, the upper surface green, composed of ± rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, with idioblasts and usually conspicuous stomata throughout, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, frequently with obscure idioblasts and stomata; ventral sporophylls hyaline to pale green, ascending, pseudopeltately attached to the axis, without or with a weakly developed adaxial flap, ovate or ovate-lanceolate, 0.8-2 × 0.4-0.85 mm, with a well-developed, denticulate keel along midrib, the base rounded, the margins hyaline, serrate to serrulate, the apex long-acuminate to shortly aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, without

conspicuous idioblasts, the stomata present only on the lower surface. Megasporangia generally in two ventral rows or at the base of ventral rows, or infrequently absent; megaspores snow-white to bone-white or yellowish with age, with or without an equatorial flange, the proximal face granular, granular-rugose, or granular-reticulate, with close reticulum of low ridges, the distal face reticulate with close to open reticulum of low to high ridges, 230-270  $\mu\text{m}$  diam. Microsporangia in two dorsal rows, frequently also on the apical region of ventral side of strobili, or strobili wholly microsporangiate; microspores tan to orange, without an equatorial flange, the proximal face micro-echinulate, the distal face baculate, 24-31  $\mu\text{m}$  diam.

HABITAT AND DISTRIBUTION: In lowland to montane forest, on open to shady roadside or stream banks, on sandy or clayish soil, on dry or moist, mossy rocks, or rocky slopes; 30-1000 m; Mexico, Guatemala, Belize, Honduras, Panama, Cuba, Jamaica, Haiti, Rep. Dominicana, Puerto Rico, Dominica, Monserrat, St. Kitts, Colombia, Venezuela, Trinidad, Tobago, and Brazil.

SELECTED SPECIMENS EXAMINED: MEXICO. COLIMA: Alzada, 4 Nov 1910, Orcutt 4640 (BM, GH). GUERRERO: Adama, Sierra Madre del Sur, N of Río Balsas, Temisco, Barranca de La Julia, 350 m, 1 Nov 1937, Mexia 8725 (BM, CAS, F, GH, K, MICH, MO, NY, UC, US), 320 m, 6 Nov 1937, Mexia 8755 (BM, F, GH, K, MO, NY, UC, US); Coyuca, Pungarabato, 28 Sep 1935, Hinton 8502



(MICH, NY, US). JALISCO: Hwy to Autlán, 9 miles N of junction at the W end of Bahía de Navidad, 300 m, 12-13 Dec 1959, McVaugh & Koelz 1727 (MICH, NY); ca. 3 km SE of Puerto Vallarta, 50 m, 12 Nov 1963, Feddema 2517 (MICH, MO); Santa Cruz de Vallarta, 300 m, 10 Dec 1926, Mexia 1276 (BM, GH, MICH, MO, NY, UC, US). NAYARIT: Bahía de Banderas, Sierra de Vallejo, La Zanja del Muerto, 20°48'N, 105°25'W, 100 m, 9 Oct 1990, G. Castillo 6069 (XAL). SINALOA: La Noria Foothills, 800 ft [244 m], 11 Oct 1925, Mexia 268½ (MO). VERACRUZ: Minatitlán, 11.4 km S de Hidalgo Amajac, sobre camino al Poblado 10, 17°20'30"N, 94°27'W, 150 m, 27 Mar 1981, Wendt et al. 3087 (NY).

GUATEMALA. IZABAL: Along Río Frío, 75 m, 17 Dec 1941, Steyermark 39925 (BM, F, US); Jocoló, 30 m, 25 Nov 1920, H. Johnson 987 (F, MICH, S, US). PETÉN: Along Río Santa Isabel, between mouth of Río Sebol and El Porvenir, 100 m, 21 Apr 1942, Steyermark 45822 (F, US), 45854 (BM, F, US).

BELIZE. CAYO: El Cayo, 13 Feb 1931, Bartlett 11457 (BM, F MICH, UC, US). TOLEDO: NE side of Blue Creek, ca. 16°14'N, 89°00'W, ca. 250 ft [76 m], 20 Mar 1989, Hill 20281 (UC); Maya Mountains, canyon along Bladen Branch from Richardson Creek to Quebrada de Oro, 16°31-33'N, 88°46-49'W, 100-200 m, 11 Mar 1987, Davidse & Brant 32309 (MO, UC).

HONDURAS. ISLAS DE LA BAHÍA: Roatán Island, 4 km E of Coxenhole, 5-20 m, 21 Apr 1967, Molina 20708 (F, NY, US).

PANAMA. CANAL AREA: Vicinity of Fort Sherman, 15 Jan 1924, Standley 31032 (US). PANAMA': Alajuela, 30-100 m, 11-12 Jan 1911, Pittier 2349 (US); 4 km

NE de Altos de Pacora, ca. 600 m, 12 Jan 1992, Valdespino 1367 (AAU, B, BM, CAS, CR, HUA, NY, PMA, QCA, UC, US); Pacora, 9 Dec 1917, Killip 2727 (US); Río Tapia, 7 Dec 1923-11 Jan 1924, Standley 26164 (BM, US), 26210 (US).

CUBA. BARACOA: Cooper's ranch, base of El Yunque Mt., Mar 1903, Underwood & Earle 302 (NY), 824 (NY). ORIENTE: Foot of El Yunque, 16 Dec 1914, Ekman 3910 (NY).

JAMAICA. CLAREDON PARISH: Aenonon Town, 2000 ft [610 m], 14 May 1950, Proctor 4498 (US). PORTLAND PARISH: John Crow Mts., ca. 10 miles SW of Priestmans River, 2500 ft [763 m], 8-10 JAN 1951, Proctor 5240 (US). TRELAWNY PARISH: Along trail WNW Quick Step to Paynes Patent, 30 Dec 1949, Proctor 3819 (US).

HAITI. L'ARTIBONITE: Vicinity of Ennery, 325-900 m, 28 Jan 1926, Leonard 9398 (K). Massif de la Hotte, Morne Rochelois, Miragoane, at Cuatre-Chemims, 1000 m, 17 Jul 1927, Ekman 8611 (K); Massif du Nord, Bayeuk, Morne Brigand, 800-900 m, 19 Dec 1924, Ekman 2957 (K).

REPUBLICA DOMINICANA. LA VEGA: 300 m, 28 Jan-7 Feb 1921, Abbott 769a (US). PACIFICADOR: Vicinity of San Francisco de Macorís, 400-100 m, 5-17 Apr 1922, Abbott 2098 (US). PUERTO PLATA: Río Sosua, 4.5 km S de la carretera Sosua-Puerto Plata, 19°45'N, 70°32'W, 20-30 m, 24 Jan 1991, Zanoni et al. 44815 (NY). SANTO DOMINGO: Villa Altagracia, ca. 150 m, 12 Feb 1930, Ekman 14287 (F, US).

PUERTO RICO. Aguas Buenas, 2 Feb 1929, N. L. Britton et al. 9192

(NY); Corozal, 13 Mar 1925, N. L. Britton et al. 8351 (NY, US); along Río Lajas, at the end of Rte 425 E of Maricao, near Salto de Curet, 18°11'N, 66°58'W, 300-350 m, 11 Jan 1992, Grimes et al. 3217 (NY); Maricao, 18 Jul 1913, Hieron (US); Mayagüez, vicinity of Mayagüez, 4-10 Mar 1906, E. Britton & Marble 545 (US); 14 miles S of San Juan, 2 Mar 1899, Mr. & Mrs. Heller 670 (NY); Sierra de Luquillo, Caribbean National Forest, road 988, 1.1 km SSE of intersection with road 191, ca. 140 m, 23 Dec 1983, Proctor & Pinto 39966 (US).

**DOMINICA. ST. ANDREW PARISH:** Between Autrou Bay and Peineville, 750 ft [229 m], 11 Sep 1965, Lellinger 339 (GH, US).

**SAINT PATRICK PARISH:** Trail to Sari-Sari Falls along Sari-Sari River from La Plaine, 1100-1300 ft [336-397 m], 31 May 1994, Hill 25723 (NY).

**MONSERRAT.** Fergus Mts., ca. 2000 ft [610 m], 30 Jan 1907, Shafer 334 (F, US); Runaway Gut, ca. 500 ft [153 m], 25 Jan 1959, Proctor 18972 (US).

**ST. KITTS.** Molyneux water source, 1000-1200 ft [305-366 m], 27 Feb 1959, Proctor 19277 (US).

**COLOMBIA. ANTIOQUIA:** Turbo, Pueblobello, Río Mulatos, 190 m, 13 Jul 1983, Santa & Brand 844 (COL). **MAGDALENA:** Santa Marta, 1898-99, H. H. Smith 2567 (F, K, MICH, NY, US).

**VENEZUELA. ANZOÁTEGUI:** Vicinity of confluence of Río León with Río Zumbador, NE of Bergatín, 400-500 m, 26 Feb 1945, Steyermark 61191 (F, US).

**CARABOBO:** Between Carabobo and Tinaquillo, 500 m, 28 Dec 1938, Alston 5746 (AAU, NY-2 sheets, QCA, US); Hacienda Stelling, Valencia, 700 m, 14 Jan 1939,

Alston 6300 (AAU, MG, NY-2 sheets, QCA). **DELTA AMACURO:** Imataca Mts., S of Santa Catalina, opposite the eastern end of Tortola Island, delta of Orinoco River, Nov 1896, Thompson 19 (US). **DIST. FEDERAL:** Galipán, Moritz 71 & 221 (BM). **LARA:** Jiménez, Parque Nacional Yacambú, Quebrada Honda, 9°41'N, 69°30'W, ca. 700 m, 28 Oct 1982, Davidse & González 21340 (MO); Jiménez, Paso de Angostura, Represa de Yacambú, confluencia de la Quebrada Honda y Río Yacambú, 9°41'N, 69°30'W, 500 m, 28-31 Jul 1973, Steyermark & Carreño 107607 (F). **MIRANDA:** Path from Petare to La Guayrita, 900 m, 11 Dec 1938, Alston 5469 (AAU, NY, QCA, US). **PORTUGUESA:** Guanare, near Desembocadero, 9°10'N, 69°53'W, ca. 400 m, 2 Nov 1982, A. R. Smith & Ortega 857 (MO). **SUCRE:** Benítez, Serranía de la Paloma, along Río Frio, between Ajíes and Guariquén, 8.5 km S of Ajíes, 10°25'N, 63°6'W, 60 m, 19 Feb 1980, Steyermark et al. 121380 (MO); El Guayabito, along Río Guayabo at its juncture with Río Zumbador, 10°10'N, 64°17'W, 20-22 Nov 1981, Davidse & González 19275 (MO); Peninsula de Paria, SW of Cerro de Humo, vicinity of Manacal, 15 km (by air) NW of Irapa, 10°41'5"N, 62°39'5"W, 800 m, 29 Nov 1979, Steyermark & Liesner 120662 (MO). **YARACUY:** Los Canelitos, caserio de San José, 3-4 Jul 1953, Aristaguieta & Pannier 1875 (US).

**TRINIDAD.** 15 Nov 1877, Fendler 108 (B, BM, CAS, F, GH, K, MICH, NY-4 sheets, UC, US, YU).

**TOBAGO. ST. GEORGE PARISH:** 3 air mi NNE of Scarborough, near Mason Hall, 1000 ft [305 m], 9 Jan 1989, Worthington & Jack 17769 (NY).

BRAZIL. MATO GROSSO: 19 May 1894, Lindman A3495 (S).

NOMENCLATURAL COMMENTS: Palisot de Beauvois (1804) described Displotachyum tenellum without citing any specimen. Poiret (1814) transferred this species to Lycopodium without citing any specimen. He mentioned, however, that the species was from "les Indes orientales." According to Reed (1965-66), this was an error for Puerto Rico since Desvaux's specimen was labeled "India occidentalis in Portorico ex Herb. Vent. Proctor (1985: 45) lectotypified S. tenella based on Desvaux's specimen. There is no evidence, however, that Desvaux's specimen was ever seen by Palisot de Beauvois. I consider, in accordance with the Code of Botanical Nomenclature (Greuter, 1994), that since no original material was cited by the original author, which may be presumed missing, a neotype may be designated rather than a lectotype. Proctor's typification, therefore, should be considered a neotypification.

TAXONOMIC DISCUSSION: Selaginella tenella has been defined here in a broader sense as to include S. subcaulescens and S. cladorrhizans. This species is chiefly characterized by having very conspicuous idioblasts on the upper surface of the leaves and sporophylls. Traditionally, S. subcaulescens has been maintained as a separate taxon because of its suberect to erect stems, whereas S. tenella and S. cladorrhizans were thought to be mostly creeping or rarely ascending. Specimens of S. cladorrhizans from Belize and Guatemala, however, have also

suberect and erect stems. A thorough examination of specimens of these three taxa throughout their ranges reveals no consistent character that may help separate them. Megaspores examined from S. tenella, S. subcaulescens, and S. cladorrhizans (see Figs. 8A-O) show only minor variations on exospore sculpturing and microstructure patterns. I have, therefore, decided to treat them as conspecific under S. tenella.

Two other species, S. humilis Jenman and S. maracasensis O. C. Schmidt, are probably conspecific with S. tenella. I have been unable, however, to secure adequate type material of S. humilis and S. maracasensis, and thus can not be completely sure of their proper status.

**30. *Selaginella leucoloma* Alston ex Crabbe & Jermy, Fern Gaz. 11: 262. 1976.**

Type: BOLIVIA. LA PAZ: [Larecaja,] Hacienda Simaco sobre el camino a Tipuani, 1400 m, Feb 1920, Buchtien 5280 (Holotype: BM!, photo: NY!, QCA!; isotype: US!).

Plants epipetric. Stems suberect to erect, stramineous or greenish, 5-15 cm long, 0.3-0.84 mm diam., not articulate, occasionally with flagelliform branches, stoloniferous, 2-4-branched. Rhizophores axillary, restricted to basalmost portion of the stem, filiform, 0.08-0.16 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded to cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves imbricate and appressed along basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem, otherwise distant apically, ascending to perpendicular to the stem, broadly ovate, ovate-oblong, or ovate-elliptic, 1.6-2.4  $\times$  1.0-1.7 mm; base rounded to subcordate, the acroscopic base strongly overlapping the stem, the basiscopic base not overlapping the stem; the leaves from basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem with the acroscopic margin broadly hyaline, fimbriate, the basiscopic margin pale green, fimbriate, the apex obtuse, ciliate at tip; the leaves from apical  $\frac{1}{2}$  to  $\frac{2}{3}$  of the stem with the acroscopic margin long- to short-ciliate along basal  $\frac{3}{4}$ , serrate to serrulate apically, the basiscopic margin pale green, infrequently ciliate at proximal base, otherwise entire to serrulate, the apex broadly acute to acute, dentate at tip, the basiscopic margin in all lateral leaves

with obscure stomata and short hairs near the margin; the upper surface glabrous, without idioblasts or stomata, the lower surface glabrous, usually with conspicuous or obscure idioblasts, and with stomata along midrib. Median leaves slightly imbricate to distant and appressed along basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem, otherwise distant and ascending apically, ovate-orbicular to ovate-deltate along basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem, otherwise ovate to ovate-elliptic apically,  $0.98-1.52 \times 0.55-0.94$  mm; base oblique or weakly subcordate, the inner base usually entire, the outer base tufted with short hairs, especially along basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem; margins broadly hyaline, fimbriate on leaves from basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem, otherwise the inner margin long-ciliate and the outer margin entire along basal  $\frac{1}{3}$ , ciliate-denticulate to serrate along apical  $\frac{2}{3}$ ; apex broadly acute and ciliate at tip on leaves from basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem, otherwise acute and dentate at tip; both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib, the lower surface without idioblasts or stomata. Axillary leaves similar to lateral leaves, except frequently long-ciliate along basal  $\frac{1}{2}$  and serrate to serrulate apically. Strobili terminal on stem and branch apices, lax, slightly flattened, weakly dorsiventral, 2-5 mm long. Sporophylls subdimorphic; dorsal sporophylls green, spreading, basally attached to the axis, without or with a weakly developed adaxial flap extending along  $\frac{1}{3}$  to  $\frac{1}{3}$  the sporophyll length, ovate,  $0.8-1.1 \times 0.36-0.56$  mm, with a well developed, denticulate to entire keel along midrib, the base rounded, the margins broadly hyaline, ciliate-denticulate along basal  $\frac{3}{4}$ , serrulate apically, the apex acute, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that



folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts, with conspicuous stomata along midrib, the lower surface silvery green, composed of elongate cells with sinuate walls, glabrous, without idioblasts or stomata; ventral sporophylls pale green, ascending, pseudopeltately attached to the axis, without an adaxial flap, ovate to ovate-elliptic,  $0.8-1 \times 0.4-0.6$  mm, with a weakly developed, entire keel along midrib, the base rounded, the margins broadly hyaline, ciliate-denticulate along basal  $\frac{2}{3}$ , serrate to serrulate apically, the apex acute, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present along midrib. Megasporangia along basal  $\frac{1}{2}$  of two ventral rows or absent; megaspores straw, baryta, or naphthalene yellow (light lemon-yellow), without an equatorial flange, the proximal face seemingly smooth or granulose near the laesura, rugulate-striate marginally, the distal face reticulate with close reticulum of low ridges,  $210-235 \mu\text{m}$  diam. Microsporangia in two dorsal rows, frequently also on the apical  $\frac{1}{2}$  of ventral side of strobili, or strobili wholly microsporangiate; microspores not studied [ca.  $37.5 \mu\text{m}$ , according to Crabbe & Jermy, 1976].

HABITAT AND DISTRIBUTION: Wet mossy mats on rocks; 1400-1769 m; Peru and Bolivia.

SPECIMENS EXAMINED: PERU. PUNO: trail from Aricoma Pass to Santo Domingo, 5800 ft [1769 m], Apr 10 1940, McCarroll 126 (MICH p.p.).

BOLIVIA. LA PAZ: [Larecaja,] Hacienda Simaco sobre el camino a Tipuani, 1400 m, Feb 1920, Buchtien 5278 (5278A at BM, and US), Buchtien 5280 (BM, photo NY, photo QCA, US, type coll. of S. leucoloma); Murillo, Valley of the Río Zongo, ca. 30 min by trail which climbs from the Cahua Hydroelectric Plant on the left bank of the Río Zongo, 16°05'S, 68°03'W, 23 Apr 1982, Solomon 7557 (MO, NY, UC). **WITHOUT SPECIFIC DEPARTMENT OR LOCALITY:** Ticunhuaya, Cordillera Real, 5000 ft [1525 m], Apr 20-24 1926, Tate 1078 (NY).

**TAXONOMIC DISCUSSION:** Selaginella leucoloma can be confused with and seems to be related to S. chionoloma and S. sobolifera. It can be distinguished from these two species chiefly by the appressed median and lateral leaves along basal  $\frac{1}{3}$  to  $\frac{1}{2}$  of the stem, which have the margins fimbriate, the apex obtuse to broadly acute and ciliate at tip, and the acroscopic margin of the lateral leaves and the margins of the median leaves broadly hyaline. Moreover, the median leaves in this basal region of the stem tend to be ovate-orbicular or ovate-deltate and have the outer base tufted with long hairs.

Megasporangia were observed to contain usually one large, well developed megaspore and three smaller and less developed ones. It is uncertain, however, whether or not the smaller ones are viable.

As described, the basal part of the stems in S. leucoloma is covered with appressed, fimbriate leaves. Some of these leaves are scale-like, a condition found typically in species that reproduce vegetatively by stolons, tubers, and flagelliform

buds. It is probable, as previously discussed in other species of subg. Heterostachys, that the erect stems arise from buds developed from flagelliform branch apices. Another possibility is that the erect stems arise from tuber-like buds originating from the stolon tips. I did not observe, however, well defined buds in either flagelliform apices or the stolon tips.

**31. *Selaginella sobolifera* A. R. Smith, Ann. Missouri Bot. Gard. 77: 269. 1990.**

Type: VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Río Cuao, Río Orinoco, Danta (Tapir) Falls, 125 m, 19 Nov 1948, Maguire & Politi 27331 (Holotype: UC!; isotypes: NY!, US-n.v.).

Plants terrestrial or epipetric. Stems suberect to erect, stramineous to greenish, 3.5-18 cm long, 0.24-0.78 mm diam., not articulate, frequently with flagelliform stem and branch apices, stoloniferous, 2- or 3-branched. Rhizophores axillary, restricted to basal  $\frac{1}{3}$  or occasionally to basal  $\frac{1}{2}$  of the stem, filiform, 0.06-0.22 mm diam. Leaves dimorphic throughout, membranous, the upper surface green, composed of polygonal to  $\pm$  rounded cells usually with strongly sinuate walls, the lower surface silvery green, composed of elongate cells with strongly sinuate walls. Lateral leaves distant, perpendicular to the stem, broadly ovate to ovate-oblong,  $1.5-2.5 \times 0.5-1.4$  mm; base rounded, the acroscopic base strongly overlapping the stem, the basiscopic not overlapping the stem; the acroscopic margin broadly hyaline, long-ciliate, ciliate-denticulate, or serrate along basal  $\frac{3}{4}$ , otherwise serrulate apically, the basiscopic margin narrowly to broadly hyaline or pale green, serrulate to entire; apex acute to acuminate, dentate at tip; the upper surface with short hairs and inconspicuous stomata near the basiscopic margin, otherwise glabrous, without idioblasts, the lower surface glabrous, usually with conspicuous idioblasts, and with stomata along midrib. Median leaves distant, ascending, narrowly elliptic,  $0.8-1.3 \times 0.4-0.64$  mm; base oblique or rounded,

occasionally the outer base tufted with few, short hairs; margins broadly hyaline, the inner margin long-ciliate or ciliate-denticulate along basal  $\frac{1}{2}$ , sparsely serrate to serrulate apically, the outer margin entire along basal  $\frac{1}{2}$ , serrate to serrulate apically, or occasionally both margins serrate to serrulate; apex gradually long-aristate, the arista  $\frac{1}{3}$  or less than  $\frac{1}{2}$  the length of the lamina, 0.16-0.46 mm long, frequently puberulent, dentate at tip, both surfaces glabrous, the upper surface without idioblasts, with stomata along midrib, the lower surface without idioblasts or stomata. Axillary leaves similar to lateral leaves, or more distinctly ovate with the margins long-ciliate along basal  $\frac{2}{3}$ , serrate to serrulate apically, and with the halves of the leaf symmetric. Strobili terminal on stem and branch apices, lax and flattened, dorsiventral, or infrequently slightly quadrangular, 2-10 mm long. Sporophylls dimorphic; dorsal sporophylls green, spreading, basally attached to the axis, with a strongly developed adaxial flap extending along  $\frac{1}{3}$  to  $\frac{1}{2}$  the sporophyll length, ovate or ovate-lanceolate,  $0.96-1.5 \times 0.38-0.58$  mm, with a strongly developed, denticulate keel along midrib, the base rounded, the margins broadly hyaline, ciliate, ciliate-denticulate, or serrate, the apex acute to acuminate, the upper surface green, composed of  $\pm$  rounded cells, except for the portion that folds to form the flap where the cells hyaline and elongate with sinuate walls, glabrous, without idioblasts, with conspicuous stomata along midrib and occasionally with some scattered apically, the lower surface silvery to silvery green, composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts or stomata; ventral sporophylls pale green, ascending, pseudopeltately

attached to the axis, with a weakly developed adaxial flap, ovate, ovate-elliptic, or elliptic,  $0.94-1.4 \times 0.44-0.6$  mm, with a well developed, denticulate keel along midrib, the base rounded, the margins broadly hyaline, long-ciliate along basal  $\frac{2}{3}$  and ciliate-denticulate apically, or ciliate-denticulate along basal  $\frac{2}{3}$  and serrate to serrulate apically, the apex long-aristate, both surfaces composed of elongate cells with sinuate walls, glabrous, without conspicuous idioblasts, the stomata present only on the lower surface along the midrib. Megasporangia in two ventral rows or abortive; megaspores massicot to naphthalene yellow, with or without an equatorial flange, the proximal face striate-rugulate to seemingly smooth, the distal face reticulate with open reticulum of moderately high ridges, 220-255  $\mu\text{m}$  diam. Microsporangia in two dorsal rows; microspores tan to orange, without an equatorial flange, the proximal and distal faces clavate, 24-39  $\mu\text{m}$  diam.

HABITAT AND DISTRIBUTION: On shaded road-, stream-, or clay banks, moist woodland, sandy soil, or on rocks in the shade or near streams; 125-1800 m; Colombia and Venezuela.

TAXONOMIC DISCUSSION: Because of its aristate and narrowly elliptic median leaves, ovate to ovate-oblong lateral leaves, usually broadly hyaline leaves, flagelliform stem and branch apices, and stoloniferous stems, S. sobolifera seems to be more closely related to and is difficult to separate from S. chionoloma. In fact, some of the specimens of S. sobolifera from Colombia have been annotated

in the past as S. chionoloma. Selaginella sobolifera differs from S. chionoloma by having ventral sporophylls with long-ciliate to ciliate-denticulate (vs. serrate to serrulate) margins, by its massicot to naphthalene yellow (not orange-buff) megaspores, and microspores under LM with the distal face clavate (vs. verrucate to seemingly smooth).

There are three collections from Vaupés in Colombia (Schultes & Cabrera 11969, 13307, both at GH!, and H. Weber 641, U!) that resemble to some degree S. sobolifera. They differ from S. sobolifera by having median leaves linear, linear-lanceolate, or linear-elliptic, sparsely serrulate, with the apex acute to short-acuminate, usually with few tufted teeth or short cilia on the outer base (although two collections of S. sobolifera var. arcana [Betancur 1383, HUA, NY; and Schultes & Cabrera 12755, GH, US] also possess them), and the sporophylls sparsely serrulate. The strobili on these collections have only microsporangia, which occupy the two dorsal rows of sporophylls, the megasporangia are abortive and occupy the two ventral rows of sporophylls. These collections perhaps deserve taxonomic recognition. However, they lack megaspores, which are critical in ascertaining species in this complex; thus I prefer not to describe them as a new species.

Selaginella sobolifera as defined here is formed by two rather distinct varieties. The morphological differences between these varieties, however, do not seem to be fundamental. In fact, megaspore and microspore samples taken from specimens representing both populations and studied under SEM and LM

respectively appear to be similar. Nevertheless, the characteristics that serve to separate them seem to correlate with their longitudinal and elevational distribution patterns.

As in many other species here discussed (including S. chionoloma), S. sobolifera propagates vegetatively by sending out stolons from the base of the erect stems. These stolons are covered with very small, greenish, and pseudoisomorphic leaves. They form rather elongate, flattened, tuber-like buds at the tip. These buds, which are frequently observed at the base of erect stems, are covered with scale-like leaves, develop into suberect to erect, aerial, branched stems, which in turn repeat the cycle.

#### Key to the varieties of Selaginella sobolifera

1. Lateral leaves with the acroscopic margin long-ciliate, the cilia ca.  $\frac{1}{2}$  the width of the lamina, the apex acuminate; ventral sporophylls with the margins long-ciliate along basal  $\frac{2}{3}$ ; median leaves with the margins or at least the inner margin long-ciliate.....31a. var. sobolifera
1. Lateral leaves with the acroscopic margin serrate or ciliate-denticulate, the cilia or teeth less than  $\frac{1}{4}$  the width of the lamina, the apex acute; ventral sporophylls serrate or ciliate-denticulate along basal  $\frac{2}{3}$ ; median leaves with the margins serrate to serrulate.....31b. var. arcana



**31a. *Selaginella sobolifera* A. R. Smith var. *sobolifera***

Type: same as the type of the species.

Illustration: Smith, 1990 (Figs. 9E-J).

Var. *sobolifera* is characterized by having lateral leaves acuminate, with the acroscopic margin long-ciliate along basal  $\frac{3}{4}$ , the ventral sporophylls long-ciliate (the cilia usually ca.  $\frac{1}{2}$  the size of the width of the leaf) along the basal  $\frac{2}{3}$ , and the median leaves frequently ciliate.

HABITAT AND DISTRIBUTION: On clay or stream banks, sandy soil, or on shaded rocks; (125-)900-1800 m; Colombia and Venezuela.

SPECIMENS EXAMINED: COLOMBIA. BOYACÁ: Cordillera Oriental, vertiente Oriental, Valle del Río Cusiana, carretera entre Pajarito y Agua Azul, 900 m, 21 Oct 1967, R. Jaramillo 3944 (COL); carretera Pajarito-Agua Azul, margen del Río Chichaca, 600 m, 14 Oct 1967, Hagemann 714 (COL). CUNDINAMARCA: Cordillera Oriental, Gazaunta Valley, 9 km NW of Medina, 975 m, 5 Oct 1944, M. Grant 10387 (COL, CR, US). NORTE DE SANTANDER: Camp 84 on pipeline, 1800 m, 16 Sep 1946, M. Foster & R. Foster 1721 (A).

VENEZUELA. BARINAS: Pedraza, above El Agarrobo [Algarrobo?], 8°31'N, 70°35'W, 400 m, 3 Aug 1983, van der Werff & R. Ortiz 5818 (MO); Pedraza, trail from Pozo Negro to Mesa de Canagua, 8°32-34'N, 70°37-40'W, 400-

600 m, 23 Nov 1990, Dorr et al. 7799 (NY, PMA, UC, VEN), 7799A (NY).  
**TÁCHIRA:** Valle situado al W de Ayari, 200 m, 27 Aug 1966, Steyermark & Rabe 96639 (GH); W of El Piñal, W of bridge over Río Frio, 250-300 m, 27-30 Aug 1966, Steyermark & Rabe 96693 (K); Río San Buena, 10 km W of La Fundación, around Represa Dorada, 7°47-48'N, 71°46-47'W, 700-1000 m, 13-15 Mar 1980, Liesner et al. 9536 (MO); Uribante, Empresa Las Cuevas near La Fundación, ca. 8°50'N, 71°47'W, 900 m, 6 Jul 1983, van der Werff 4923 (MO); Uribante, en los alrededores del campamento Siberia (CADAPE), 8°01'N, 71°43'W, 1200 m, 19 Nov 1985, Ortega & van der Werff 2809 (UC), Cerro Las Lomas, 8°01'N, 71°45'W, 1300 m, 20 Nov 1985, Ortega & van der Werff 2833 (UC); Uribante, along road from La Siberia to entrance to Las Cuevas Represa, 10 Jul 1983, van der Werff & González 5271 (MO); Uribante, ca. 3 km outside of Siberia on road to Pegonero, ca. 8°55'N, 71°40'W, ca. 1300 m, 11 Jul 1983, van der Werff & González 5377 (MO, UC). **TERRITORIO FEDERAL AMAZONAS:** Río Cuao, Río Orinoco, Danta (Tapir) Falls, 125 m, 19 Nov 1948, Maguire & Politi 27331 (NY, UC, type of S. sobolifera var. sobolifera).

**31b. *Selaginella sobolifera* A. R. Smith var. *arcana* Valdespino, var. nov.**

Type: COLOMBIA. CUNDINAMARCA: Medina, 500-550 m, 19 Jun 1986,

Murillo & Harker 2186 (Holotype: NY!; isotype: MO!).

A var. sobolifera foliis lateralibus apice acutis, margine acroscopico serratis vel ciliatis-denticulatis, ciliis et dentibus minus quam  $\frac{1}{4}$  latitudinibus laminae, foliisque intermediis marginibus serratis vel serrulatis diversa.

L., arcanus, shut up, secret, mysterious, private; referring to its rather concealed identity.

This variety is characterized by having the acroscopic margin of the lateral leaves and the margins of the ventral sporophylls serrate to ciliate-denticulate, if ciliate-denticulate then the cilia length less than  $\frac{1}{4}$  the width of the lamina, the margins of the median leaves serrate, and the apex of the lateral leaves acute.

HABITAT AND DISTRIBUTION: On shaded road- or stream banks, moist woodland, or on rocks; southwestern range of the species, more precisely the southwestern part of Colombia, and is found mainly at 250-550(-800) m.

SPECIMENS EXAMINED: COLOMBIA. BOYACÁ: Llanos Aguasclaras, 400 m, Apr 1963, Saravia 2673 (COL). CAQUETÁ: Florencia, ca. 420 m, Dec 1930, E. P. Arbeláez 627 (BM, US); Florencia, Morelia, ribera del Río Bodoquero, 300 m, 26 Jun 1987, Santa 1257 (AAU, HUA); Florencia, Quebrada La Perdiz, 300 m, 23 Jun 1987, Santa 1220 (AAU); Florencia, Río Hacha, 300 m, 23 Jun 1987, Santa 1225 (AAU); Transecto Neiva-San Vicente del Caguán, E y arriba de Río Pato,

ca. 2°30-33'N, 74°45'W, 460-480 m, 1 Dec 1990, S. Churchill & J. Betancur 16999 (NY). CUNDINAMARCA: Cordillera Oriental, Buena Vista, Gazaguan [Gazaunta] Valley, 6 km W of Medina, 800 m, 6 Oct 1944, M. Grant 10412 (COL, CR, US-2 sheets); Medina, 500-550 m, 19 Jun 1986, Murillo & Harker 2186 (MO, NY, type coll. of S. sobolifera var. arcana). META: Mesetas, Inspección de Policía La Uribe, Vereda La Lagartija, entre La Lagartija y El Diviso, 3°7.4'N, 74°18.03'W, 460 m, 13 Aug 1989, J. Betancur 1383 (HUA, NY); San Juan de Arama, Parque Nac. Nat. Sierra de la Macarena, estación La Curia, Cerro El Tablazo, vertiente del Río Güejar, 480-650 m, 20-30 Sep 1987, A. Fernández et al. 7646 (COL). VAUPÉS: Soratama, entre Río Pacoa y Río Kananari [Cananari], ca. 250 m, 21 Jun 1951, Schultes & Cabrera 12755 (GH, US).

COUNTRY UNKNOWN: André K426 (K).

TAXONOMIC DISCUSSION: Alston et al. (1981) referred Schultes & Cabrera 12755 (GH, US) to S. cladorrhizans (= S. tenella), but that species usually has very conspicuous idioblasts on the upper surface of the leaves, and white (not massicot to naphthalene yellow) megaspores.

## APPENDICES

APPENDIX I  
SPECIES INCERTAE SEDIS

***Selaginella orizabensis*** Hieronymus, *Hedwigia* 41: 193. 1902.

Syntypes: MEXICO. VERACRUZ: ~Orizaba, 1853, F. Müller [ex herb. Schlumberger] (B, probable NY); near Eugenio, Mountains of Sierra de San Cristobal, Dec 1853, Sartorius? [ex herb. Schultz-Bipont.] (presumably at B).

This is little-known species originally described from Orizaba in Veracruz, Mexico. I have seen a specimen at NY labeled "1853, Müller 258", in a printed label, and "Orizaba, 1855 Müller," in a handwritten label. It matches the protologue of *S. orizabensis* and could be part of the original material. Hieronymus (1904) does not give a clear indication as to where the syntypes were located, but presumably they should be at B, where he used to work. These syntypes were not among the types I received in loan from B.

## APPENDIX II

### EXCLUDED TAXA

1. There is a South American taxon not described in this conspectus that appears to be a new species, probably belonging to subg. Heterostachys. It is represented by several collections from Colombia, Venezuela, and Ecuador, most of which were previously determined as S. microphylla (Kunth) Spring. Selaginella microphylla is distinct from the, presumed, new species and is not considered here to belong to subg. Heterostachys. Selaginella microphylla has, however, several synonyms, the type of some of which I have not seen. I am, therefore, unsure as to the correct status for the presumed new taxon and prefer not to describe it at the present time.

2. Some specimens of Selaginella from South America currently referred to as S. novae-hollandiae (Swartz) Spring, a widely distributed species in the continental region of the Neotropics, may prove to be better classified in subg. Heterostachys, probably as a new species. Unfortunately, S. novae-hollandiae as currently applied, seems to be an ill-defined species and its type has not been located. Therefore, a formal decision regarding the taxonomic status of those specimens must await a thorough search for Swartz' type, which could be found within the Swartz herbarium at S.

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APPENDIX IV

DISTRIBUTION OF *SELAGINELLA* SUBG. *HETEROSTACHYS* SPECIES

IN CENTRAL AND SOUTH AMERICA

| Taxa <sup>1</sup> | M<br>e<br>x <sup>2</sup> | G<br>u<br>a | B<br>e<br>l | H<br>o<br>n | E.<br>S. | N<br>i<br>c | C.<br>R. | P<br>a<br>n | W.<br>I. <sup>3</sup> | C<br>o<br>l | V<br>e<br>n | T.<br>&<br>T. | G<br>u<br>y | S<br>u<br>r | F.<br>G. | E<br>c<br>u | P<br>e<br>r | B<br>r<br>a | B<br>o<br>l | P<br>a<br>r | A<br>r<br>g | U<br>r<br>u |
|-------------------|--------------------------|-------------|-------------|-------------|----------|-------------|----------|-------------|-----------------------|-------------|-------------|---------------|-------------|-------------|----------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| bern              | ●                        | ●           | ●           | ●           | ●        | 4           |          |             |                       |             |             |               |             |             |          |             |             |             |             |             |             |             |
| broa              |                          |             |             |             |          |             |          |             |                       |             |             | ●             |             |             |          |             |             |             |             |             |             |             |
| cavi              |                          |             |             |             |          |             |          |             |                       | ●           | ●           |               |             |             |          | ●           |             |             |             |             |             |             |
| chio              |                          |             |             |             |          |             |          |             |                       |             |             |               |             |             |          |             | ●           |             | ●           |             |             |             |
| corr              |                          |             |             |             |          |             |          | ●           |                       |             |             |               |             |             |          |             |             |             |             |             |             |             |
| fini              | ●                        |             |             |             |          |             |          |             |                       |             |             |               |             |             |          |             |             |             |             |             |             |             |
| flac              |                          |             |             |             |          |             |          |             |                       |             | ●           |               |             |             |          |             |             |             |             |             |             |             |
| flag              | ●                        | ●           | ●           | ●           |          | ●           | ●        | ●           | ●                     | ●           | ●           | ●             | ●           | ●           | ●        | ●           | ●           | ●           | ●           |             |             |             |
| glos              |                          |             |             |             |          |             |          |             |                       |             |             |               |             |             |          |             |             |             | ●           |             |             |             |
| gyno              |                          |             |             |             |          |             |          |             |                       |             | ●           |               | ●           |             | ●        |             |             |             |             |             |             |             |
| hyal              |                          |             |             |             |          |             |          |             |                       |             | ●           |               |             |             |          |             |             |             |             |             |             |             |
| karo              |                          |             |             |             |          |             |          |             |                       |             |             |               | ●           |             |          |             |             |             |             |             |             |             |
| leuc              |                          |             |             |             |          |             |          |             |                       |             |             |               |             |             |          |             | ●           |             | ●           |             |             |             |

Appendix IV (continued)

| Taxa <sup>1</sup> | M<br>e<br>$\chi^2$ | G<br>u<br>a | B<br>e<br>l | H<br>o<br>n | E.<br>S. | N<br>i<br>c | C.<br>R. | P<br>a<br>n | W.<br>I. <sup>3</sup> | C<br>o<br>l | V<br>e<br>n | T.<br>&<br>T. | G<br>u<br>y | S<br>u<br>r | F.<br>G. | E<br>c<br>u | P<br>e<br>r | B<br>r<br>a | B<br>o<br>l | P<br>a<br>r | A<br>r<br>g | U<br>r<br>u |
|-------------------|--------------------|-------------|-------------|-------------|----------|-------------|----------|-------------|-----------------------|-------------|-------------|---------------|-------------|-------------|----------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| line              | •                  | •           |             |             |          |             |          |             |                       |             |             |               |             |             |          |             |             |             |             |             |             |             |
| lych              |                    | •           |             |             |          |             | •        |             |                       | •           | •           |               |             |             |          |             |             |             |             |             |             |             |
| maci              |                    |             |             |             |          |             |          |             |                       |             |             |               |             |             |          | •           | •           |             |             |             |             |             |
| mini              | •                  |             |             | •           |          | •           |          | •           |                       |             | •           | •             |             |             | •        |             |             | •           | •           |             |             |             |
| mixt              | •                  |             |             |             |          |             |          |             |                       |             |             |               |             |             |          |             |             |             |             |             |             |             |
| mori.a            | •                  | •           |             | •           |          |             | •        | •           |                       | •           | •           |               |             |             |          | •           |             |             |             |             |             |             |
| mori.b            |                    |             |             |             |          |             |          |             |                       | •           | •           |               |             |             |          |             |             |             |             |             |             |             |
| mori.c            |                    |             |             |             |          |             | •        |             |                       | •           | •           |               |             |             |          | •           | ?           |             |             |             |             |             |
| musc              |                    |             |             |             |          |             |          |             |                       |             | •           | •             |             |             | •        |             |             | •           |             | •           | •           |             |
| popa              | •                  | •           |             |             |          |             | •        | •           |                       | •           | •           |               |             |             |          |             |             |             | •           |             |             |             |
| pore              |                    |             |             |             |          |             | •        | •           | •                     | •           | •           | •             | •           |             | •        | •           |             | •           |             |             |             |             |
| porp              | •                  | •           |             | •           | •        | •           | •        | •           |                       | •           | •           |               |             |             |          | •           |             |             |             |             |             |             |
| prol              | •                  |             |             |             |          | •           |          |             |                       |             |             |               |             |             |          |             |             |             |             |             |             |             |
| ramo              |                    |             |             |             |          |             |          |             |                       |             |             |               |             |             |          | •           | •           |             |             |             |             |             |
| seem              |                    |             |             |             |          |             |          | •           |                       | •           |             |               |             |             |          | •           | •           | •           |             |             |             |             |
| simp              | •                  |             |             |             |          |             | •        |             |                       |             | •           | •             |             |             |          |             |             | •           | •           |             |             |             |
| sobo.a            |                    |             |             |             |          |             |          |             |                       | •           | •           |               |             |             |          |             |             |             |             |             |             |             |

Appendix IV (continued)

| Taxa <sup>1</sup> | M<br>e<br>x <sup>2</sup> | G<br>u<br>a<br>t<br>e<br>m<br>a<br>l<br>a | B<br>e<br>l<br>i<br>z<br>e | H<br>o<br>n<br>d<br>u<br>r<br>a<br>s | E.<br>S. | N<br>i<br>c<br>a<br>r<br>a<br>g<br>u<br>a | C.<br>R. | P<br>a<br>n<br>a<br>m<br>a | W.<br>I. <sup>3</sup> | C<br>o<br>l<br>o<br>m<br>b<br>i<br>a | V<br>e<br>n<br>e<br>z<br>u<br>e<br>l<br>a | T.<br>&<br>T. | G<br>u<br>y<br>a<br>n<br>a | S<br>u<br>r<br>i<br>n<br>a<br>m | F.<br>G. | E<br>c<br>u<br>a<br>d<br>o<br>r | P<br>e<br>r<br>u | B<br>o<br>l<br>i<br>v<br>i<br>a | P<br>a<br>r<br>a<br>g<br>u<br>a<br>y | A<br>r<br>g<br>e<br>n<br>t<br>i<br>n<br>a | U<br>r<br>u<br>g<br>u<br>a<br>y |
|-------------------|--------------------------|-------------------------------------------|----------------------------|--------------------------------------|----------|-------------------------------------------|----------|----------------------------|-----------------------|--------------------------------------|-------------------------------------------|---------------|----------------------------|---------------------------------|----------|---------------------------------|------------------|---------------------------------|--------------------------------------|-------------------------------------------|---------------------------------|
| sobo.b            |                          |                                           |                            |                                      |          |                                           |          |                            |                       | ●                                    |                                           |               |                            |                                 |          |                                 |                  |                                 |                                      |                                           |                                 |
| sten              | ●                        | ●                                         |                            |                                      |          |                                           |          |                            |                       |                                      |                                           |               |                            |                                 |          |                                 |                  |                                 |                                      |                                           |                                 |
| tene              | ●                        | ●                                         | ●                          | ●                                    |          |                                           |          | ●                          | ●                     | ●                                    | ●                                         | ●             |                            |                                 |          |                                 |                  | ●                               |                                      |                                           |                                 |
| tube              | ●                        |                                           |                            |                                      |          |                                           | ●        |                            |                       |                                      |                                           |               |                            |                                 |          |                                 |                  |                                 |                                      |                                           |                                 |

1. Species names arranged in the same order as in Appendix III. The first four letters correspond to species names, and names followed by a period and a letter correspond to varieties.

2. Abbreviation of country names correspond to the following countries: Mex = Mexico, Gua = Guatemala, Bel = Belize, Hon = Honduras, E.S. = El Salvador, Nic = Nicaragua, C.R. = Costa Rica, Pan = Panama, W.I. = West Indies, Col = Colombia, Ven = Venezuela, T. & T. = Trinidad and Tobago, Guy = Guyana, Sur = Surinam, F. G. = French Guiana, Ecu = Ecuador, Per = Peru, Bra = Brazil, Bol = Bolivia, Par = Paraguay, Arg = Argentina, Uru = Uruguay.

3. See species description for complete distribution data for species also occurring in the West Indies.

4. ● = present, ? = distribution data dubious.

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## AUTOBIOGRAPHICAL STATEMENT

Iván Alberto Valdespino Q. was born in Panamá City, Panama on December 30 of 1963. Iván is the second son of Antonio Valdespino and Althea Quintero de Valdespino. He obtained his Junior School Certificate and Secondary School Diploma from the Instituto Dr. Alfredo Cantón in San Miguelito, Panama. He then enrolled at the University of Panama, where in 1988 he obtained the degrees of Licenciado en Biología con Especialización en Botánica (BA in Biology with a major in Botany) and of Profesor de Segunda Enseñanza con Especialización en Biología (High School Teacher Certification in Biology).

At the Botany Department of the University of Panama, he worked first as auxiliary staff and then as Junior Research Assistant in the Herbarium. During this period he also worked in two projects as research assistant at the Smithsonian Tropical Research Institute in Panama (STRI). In addition, he received an Exxon Research Fellowship from STRI that enable him to conduct the field work necessary for his Bachelor's degree thesis.

It was during Iván's years as a Botany student at the University of Panama and after taking plant systematics with Professor Mireya D. Correa A. that he was captivated by ferns and fern allies, and decided to make the study of these interesting and engaging plants his lifelong interest. In order to pursue this interest he applied for and received a New York Botanical Garden Graduate Fellowship in 1988. This has enabled him to conduct studies towards a doctorate

degree at The City University of New York/New York Botanical Garden Graduate Program. In February 24 of 1995 he completed all the requirements to obtain his Doctor of Philosophy degree in Botany from the Graduate School of The City University of New York.

On March of 1995 he joined the staff of the California Academy of Sciences in San Francisco, California, as the 13<sup>th</sup> Tilton Postdoctoral Fellow, where he is continuing his revisionary studies on the genus Selaginella.

He is associated with several scientific societies including: American Fern Society, American Society of Plant Taxonomists, Asociación Latinoamericana de Botánica, Asociación Latinoamericana de Pteridología (as a founding member), International Association of Pteridologists, and Asociación Panameña de Botánica.