A MONOGRAPH OF THE FERN GENUS JAMESONIA1

ALICE F. TRYON

#0019705

Jamesonia is a well known genus, classically cited for the peculiar, indeterminate linear, habit of the leaves, but the species have been much neglected. Specimens have accumulated in herbaria for some two hundred years since Joseph de Jussieu collected a few leaves of it in Peru, sometime between 1747 and 1777. Many specimens were added during the European expeditions to South America by Karsten, Lehmann, Lindig, Née, and Schlim and they have increased more rapidly during the past thirty years through the collections of Asplund, Barclay, Cuatrecasas, Killip, Smith, and Schultes. Most of the botanists on the Cinchona Mission of the Foreign Economic Administration collected members of the genus and the South American botanists Bües, Cárdenas, Fernandez-Perez, Idrobo, Jahn, Vargas, Vareschi have added new records and collections of special interest. There is still need for complete specimens and distribution records from many areas but there has accumulated a sufficient number of collections to survey the species and to understand the relationship of the genus to others.

In this pursuit, I am indebted to many. In the search for type material in the herbaria of Europe, I was especially aided by Drs. J. Dandy, C. Jermy and by J. Crabbe at the British Museum; at Kew, Mr. F. Ballard facilitated the photographing of specimens; at Paris Drs. M. Tardieu-Blot and A. Lourteig were most helpful in locating type material; Dr. K. Kramer, at Utrecht has made suggestions on the geographic discussion; Prof. E. Asplund at Stockholm has generously shared duplicates of his collections and observations of these plants in Ecuador; at Berlin, Dr. D. Meyer was helpful in the study of the material arranged by Hieronymus; at Leningrad, Prof. B. Schischkin and A. Brobrov were most cooperative in locating and photographing the collections of Karsten.

It is with special pleasure that I recollect the many kindnesses received while collecting in Venezuela and Colombia. Drs. J. Steyermark and L. Aristeguieta expedited our trip to Mérida, Venezuela and at the University de los Andes

¹Grant G18906 from the National Science Foundation has supported the field studies and collections in Venezuela and Colombia and the cost of the illustrations.

there, Drs. C. Liscano and L. Luna of the Facultad de Ciencias Forestales generously helped us with transportation. I was fortunate to meet at Mérida, Dr. F. Tamayo who has made many collections on the páramos.

The collections and data I obtained in Colombia are abundant and for these I am most indebted to Dr. A. Fernandez-Perez who made our trip there a successful and pleasant one. My special thanks are expressed to Maria T. Murillo whose cheerful company carried us through the bad weather of the paramos. The Padres G. Huertas and L. Camargo took us to and discussed the vegetation of the paramos they know especially well around Zipaquira. In southern Colombia, in Popayan, we were fortunate to meet the Colombian ornithologist, F. C. Lehmann, who continues the interests of his famous grandfather, the botanical collector, in the natural history of this region.

I am grateful to the Curators of the herbaria cited for the loan of specimens for extended study. The abbreviations of the herbaria are from Index Herbariorum, The herbaria of the world, fourth edition, 1959, by J. Lanjouw and F. A. Stafleu.

I am especially appreciative of the help of Dr. Yu-Chen Ting, Research Fellow of the Bussey Institution, with the analysis of the chromosomes and the photograph of them; of Dr. Robert Foster for his considerable emendation of my Latin; and for his good company and council throughout the study I am indebted to my husband, Rolla Tryon.

HISTORY OF THE GENUS

The genus is named for William Jameson, born in Edinburgh in October, 1796. He was trained there in medicine and, soon after receiving his degree from the Royal College of Surgeons, became a surgeon on a whaler bound for Baffin's Bay. His first collections out of Scotland were made on Hare Island on that voyage, and he refers to his observations of arctic plants in his later work treating the alpine flora of the Andes. In 1820 he became surgeon on a ship bound for South America, landing first at Rio and then Callao. He left the ship to stay at Lima and later at Guayaquil and in 1826 he moved to the more salubrious climate of Quito. There he was appointed Professor of Chemistry and Botany at the University and later became Assayer of the

Mint and Director and Treasurer. In 1864 he was appointed by the Ecuadorian government to undertake botanical explorations and prepare a Flora of Ecuador. His three volumes, Synopsis Plantarum Aequatoriensium, printed in Quito, dated 1865, are notable as the first botanical work to be issued from the press in Quito, and the work was well reviewed by the Chilian botanist, Philippi. The Order Caballero of Spain was conferred upon him by Queen Isabella in 1867. He visited Edinburgh and London in 1872 and was entertained by J. D. Hooker and Bentham. He returned to South America early in 1873 and died, in Quito in June of that year, from fever contracted on the return voyage. His numerous collections were sent particularly to W. Hooker. This genus as well as many species of ferns and flowering plants commemorate his name and his contribution to our knowledge of the South American flora.

Hooker and Greville proposed the genus with one species, Jamesonia pulchra, in Icones Filicum (1830) from a collection sent by Jameson. In the addenda of the work they substituted for Jamesonia pulchra, a new combination Jamesonia imbricata, based on Pteris imbricata Swartz. They note that Kaulfuss called their attention to the earlier name although the description of this was not correct for their material. Indeed it was not, for Pteris imbricata is based on a collection of Joseph Jussieu from Peru and differs from Jameson's which is actually a mixture of two other species.

Gustav Kunze was the first to treat several species of Jamesonia with much thoroughness. In his sketch of the genus (1844) and in Die Farrnkraüter (1846) he described four new species including details of the stele, the orientation of the pinnae, the number of cells in the annulus and stomium and made comparisons between the species. Soon after, J. F. Klotzsch in his contributions to the flora of equatorial regions of the New World (1847), reduced Jamesonia to one of six sections under Gymnogramma. His sections are unsatisfactory in light of our present information but the classification of Jamesonia in a subgeneric rank was a progressive idea and set a precedent for subsequent work. The first botanist to study the plants in the field was H. Karsten. He described five new species in the Flora Columbiae (1862-65) from his collections in Venezuela and Colombia and made reference to the aspect of living plants.

His interest in the chemical composition of plant material is evident from the report of the glands, especially abundant on the young leaves, bearing stearoptene, soluble in alcohol. The excellent plates in this work, drawn by Düwel, are the finest done for the genus and have been reproduced in several later works.

In the fifth volume of Species Filicum (1864) by W. J. Hooker, Jamesonia was compressed into one species, Jamesonia imbricata, with four varieties. In his Reliquiae Mettenianae (1868) M. Kuhn recognized six species (under Gymnogramma) and in his studies of the Chaetopterides (1882) he treated these along with others in a new genus, Psilogramme.

Jamesonia was taken up again with eight species by L. Diels in his treatment of the Polypodiaceae (1899) in Die Natürlichen Pflanzenfamilien. Two new species were described by G. Hieronymus in his Plantae Lehmannianae (1904) in Gymnogramma, under section Jamesonia and although he published no more on them his organization and annotations of the specimens in the herbarium at Berlin illustrate an understanding of the group. In F. O. Bower's morphological studies on the Polypodiaceae (1928), the gymnogrammoid ferns were divided into four groups and the inclusion of Jamesonia in the first group of relatively primitive genera is based largely on the reports of J. M. Thompson (1918). Unfortunately these reports are erroneous in regard to the acrostichoid condition of the sporangia and the spore number 56-72 per sporangium.

C. Christensen in his classification of the Filicinae (1938) placed Jamesonia in its most natural alliance with Gymnogramma and Pterozonium, in the Chaetopterides in the tribe Gymnogrammeae of the Polypodiaceae. He remarked that Jamesonia is hardly different from Gymnogramma. In his review of the classification of Leptosporangiate ferns (1946), R. E. Holttum treated Jamesonia in Adiantaceae and followed Bower's classification of it in a group of primitive genera of the gymnogrammoid ferns, apart from Gymnogramma. In Genera Filicum (1947), E. B. Copeland places Jamesonia and Pterozonium after Eriosorus, the nomenclatorially correct name replacing Gymnogramma, in the Pteridaceae, along with 60 other genera.

Most recent studies of Jamesonia are represented by

unpublished notes accompanying herbarium specimens in the United States National Herbarium, by W. R. Maxon (although he published two new species) and in the British Museum, by A. H. G. Alston. The ample collections of Jamesonia from Venezuela and Colombia made by Alston in 1939 are complete ones and illustrate some variants of special interest.

Comparative surveys of the species of Jamesonia virtually cease with the work of Karsten in 1865 and subsequent studies are either descriptions of a few new species or concern the generic classification with little new information that would contribute to a more satisfactory classification.

COMMENTS ON THE GENUS AND SPECIES

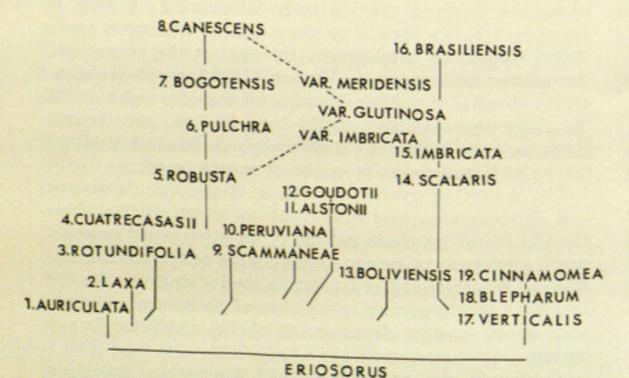
The Old World genera of gymnogrammoids, Syngramma, Craspedodictum and also Taenitis, have been considered as a natural group by both Copeland and Holttum. These have bristle-like rhizome trichomes similar to those of Jamesonia, Eriosorus and Pterozonium; the spores are clear or white, with the proximal face round or sub-triangular in outline and smooth or nearly so (in Taenitis blechnoides there is a circumferential wing above the midplane on the proximal face); venation is predominately reticulate; sori extend along the veins or are variously interrupted on them in clusters or bands parallel to the margins; sporangia are in mixed stages of development throughout the sorus; and paraphyses are numerous. Manton (1958) reports a chromosome count of n = 44 in Taenitis blechnoides and n = 116 for Syngramma quinata, both from Malaya, and regards them as quite different cytologically. A detailed study of these Old World genera would be of much interest.

The American gymnogrammoids, Eriosorus, Jamesonia and Pterozonium, constitute a natural group distinct from the Old World genera in pattern of venation, soral arrangement, alignment of sporangia, indument of the lamina, and spores. Whether similarity of rhizome indument in the Old and New World genera is evidence of an ancient relationship or of parallel development of the character is not

certain.

Jamesonia can be distinguished among the American genera by the linear leaves, usually indeterminate and once pinnate, often densely tomentose with pinnae usually entire

and imbricate. There are at least two elements of the genus more closely related to species of Eriosorus than they are to each other. The phyletic chart will serve to illustrate these and to summarize the relations discussed in this and the following paragraphs. One of the elements comprised of J. verticalis, J. blepharum and J. cinnamomea differs from the other species in having the lamina apex often determinate, the rachis base sulcate, pinnae adnate or with short, broad stalks, rigid herbaceous or coriaceous, somewhat rectangular epidermal cells having walls scarcely undulate, pinna margins ciliate, and dark brown spores. There are resemblances in these characters to Gymnogramma Mathewsii, G. longipetiolata, G. rufescens and G. setulosa which have not been transferred to Eriosorus. The second element consists of largely diverse species some of which may be independently derived from Eriosorus. They are characterized by usually indeterminate leaves with the rachis terete or trigonus, pinnae with relatively long stalks, herbaceous with elongated or roundish epidermal cells having deeply undulate walls, pinnae usually with broad borders and tan or light brown spores. There are some resemblances to Eriosorus elongatus in these characters. J. auriculata is most closely related to Eriosorus and with two others, J.



Phyletic chart of Jamesonia showing two separate lines from Eriosorus at the right and left with related species placed as explained in the text. The broken lines connect taxa which have probably hybridized.

115

laxa and J. rotundifolia, form a relatively unspecialized group.

Four species J. robusta, J. pulchra, J. bogotensis, and J. canescens have broad, membranous, dentate borders and dense tomentum on the lower pinna surface and form a closely related series. On the basis of light colored spores and dense tomentum, J. Scammanae seems to belong with this group but it has nearly subsessile pinnae with the borders entire and of a firm texture. J. Alstonii and J. Goudotii are closely related species distinguished from the others by coriaceous pinnae with sparse tomentum, or none, on the under surface. J. peruviana and J. boliviensis are similar to these in having little or no indument on the lower pinna surface. The latter is distinct in the genus in having short, erect, one or few celled trichomes, similar to those in Eriosorus elongatus on all surfaces of the pinna and margin. J. imbricata var. meridensis and var. imbricata are considered as intermediates between var. glutinosa and other species. Although J. brasiliensis is distinguished in having thin, herbaceous pinnae with strongly enrolled margins, in the patelliform shape, truncate base and bent stalks of the pinnae, it is similar to J. imbricata var. glutinosa. On these characters the latter two and J. scalaris form a separate group somewhat intermediate to the J. verticalis and J. auriculata groups.

The rigorous páramo habitat has undoubtedly influenced the reduced leaf form in Jamesonia. Isolation is a conspicuous feature of the páramos although the wide geographic distribution of several species reflects more continuous ranges in the past. Interruption and reconvergence of ranges and populations in these highlands would likely fluctuate along with climatic changes accompanying Pleistocene glaciation. Adjustment to these changes in environment seems to have been through changes especially in the reduction of the leaves. This is illustrated in J. Cuatrecasasii in which the pinnae are drawn close together by short stalks fixed to the upper pinna surface. This is a unique adaptation in a largely isolated species which, in other characters, resembles more widely distributed ones.

Interspecific hybridization, perhaps brought about through adjustments of geographic ranges in response to the changing environment, has been another evolutionary mechanism. Intermediates occur in some areas where species grow together and there are also some intermediates with *Eriosorus*. The report of the hexaploid number n = 87 for *J. bogotensis* suggests that polyploidy and hybridization both have been operative in the genus.

The species of Jamesonia represent at least two and perhaps more distinct lines which seem to have come from Eriosorus. These reticulate relationships, as well as hybridization between the genera, support the idea that the species now treated as Jamesonia and Eriosorus belong in a single genus; the groups in Jamesonia representing some specialized elements of the larger unit. The combination of these genera necessitates no changes in nomenclature, for the species treated here, since Jamesonia is the earlier name. However, the transfer of species at present in both Gymnogramma and Eriosorus to Jamesonia is best delayed until a survey of these is completed.

The species concept that I have adopted is the evolutionary one given by Simpson (1961) as a lineage evolving separately from others with its unitary evolutionary role and tendencies. The lineages are surmised from the morphological similarities of the plants and the morphological discreteness of one group of similar plants from another and thus are consistent with the evolutionary definition.

Since polyploidy has evidently been operative in the group, the full clarification of relationships awaits further cytological evidence. The relationships as presented in the present paper are for the most part drawn from comparisons of the various kinds of similarities and differences observable among the taxa. The species are to some degree comparable although they are not equally distinctive. Most of them, such as J. Cuatrecasasii, J. auriculata, J. Scammanae, J. scalaris, J. boliviensis, J. brasiliensis, and J. peruviana are quite discrete. Species such as J. robusta, J. bogotensis, J. canescens and J. pulchra are closer to each other. The greatest similarities and fewest differences exist between J. Alstonii and J. Goudotii and between J. verticalis, J. blepharum and J. cinnamomea. Within these two groups the species are very close although the relationships are not the same. Between the latter three there are intermediate specimens which appear to form a continuous series although the extreme type of each is distinct and the intermediates are

few. In J. Alstonii and J. Goudotii the differences are comparatively slight but there are no intermediates. It is possible that these might be better regarded as subspecies but I have treated them as species since they differ in several characters. Less distinctive taxa have been recognized as varieties under J. imbricata and hybridization involving them is presumed to be present. The taxonomic disposition of J. imbricata var. imbricata and var. meridensis rests upon morphological similarity with var. glutinosa. In regard to the taxonomic treatment of hybrids, I am in agreement with the remarks made by F. R. Fosberg (1961), "... hybridity is merely a matter of origin, or putative origin of the population, and its taxonomic disposition would not be determined by this, but by its morphology and behavior as a population just as with any other entity. It may well have characters which place it closer to one parent than the other".

ECOLOGY AND GEOGRAPHIC DISTRIBUTION

Jamesonia occurs from southern Mexico to central Bolivia and Brazil mainly on páramos or on cool, wet highlands at altitudes ranging from 1500-5000 meters (Map A).

The ecological data on collections of Jamesonia usually includes the term paramo which has not been precisely defined. It is generally applied to the Andean highlands south to Ecuador, between 3200 and 5000 m., above the forests and below the permanent snow, and includes the shrubby zone sometimes called páramillo or subparamo. The composite genus Espeletia characterizes the vegetation and its southern limit in Ecuador also delimits the paramo. Jamesonia is included among the genera distinguishing the páramo. The critical environmental factors to which the vegetation of the paramo is adapted are wind, strong insolation, high moisture in the soil and in the air in the form of clouds or fog, and cool temperatures ranging usually from 12° C. to -2° C. At the highest altitudes there are diurnal fluctuations in temperatures with freezing during the night. Dry seasons are mentioned for some páramos. In some species of Jamesonia, particularly J. laxa, there are growth zones on the leaves which evidently are the result of periodic growth.

There are several accounts of the vegetation of the Andean



PLATE 1. Páramo near Laguna de Anteojos, 4000 m., above Mérida, Venezuela. J. imbricata var. meridensis (lower right) at the base of a large rock, and rosettes of the Composite, Espeletia.

region which include portions on the páramo — the phytogeographic sketch of Latin America by A. C. Smith and I. M. Johnston (1945), a description of the large Páramo de Sumapaz, south of Bogotá by F. R. Fosberg (1944) and geobotanical observations of Colombia by J. Cuatrecasas (1934). In each of these there are excellent photographs of the páramo, and in the last, one of *Jamesonia* in fine detail.

Jamesonia is not restricted to the páramo or its subdivisions but I found it without exception and often in abundance on five páramos on which I collected in 1961 in the states of Mérida and Táchira, Venezuela and on ten of them in the departments of Caldas, Cauca, Cundinamarca and Huila, Colombia. On these it occurs frequently in soil at the base of rocks and boulders (plate 1) and sometimes in open grassy meadows growing with rhizomes deeply embedded in the grassy turf. In some cases the grassy areas are known to be burned and presumably the rhizomes are resistant to this. Several species grew in the open soil along road cuts which indicates the ability of these plants to establish them-

selves in newly available areas.

The páramos above Mérida are readily accessible by cable car covering 12.5 kilometers and 3125 meters altitude in a few minutes. The terrain is irregular here with several small glacial lakes and towering snow covered peaks, Espejo, Bolivar, Humboldt, and Bonpland. In mid-September there was heavy rain and fog in the afternoon and sometimes snow. J. canescens was abundant here in scattered colonies between 3400 and 4000 meters (plate 2). It was usually among rocks but also on grassy slopes where the leaves were more slender with delicate petioles and whiter tomentum. J. imbricata var. meridensis was less frequent but in large colonies growing near J. canescens. Cystopteris fragilis (L.) Bernh., Polypodium peruvianum Desv., Blechnum loxense (HBK.) Hieron., Lycopodium contiguum Kl. and species of Elaphoglossum and Polystichum also occurred there. Compositae were the most conspicuous of flowering plants with both the white and yellow flowered Espeletia, Senecio, Baccharis being common. Other families were represented by Echeveria, Lobelia, Castilleja, Sisyrinchium and Gentiana. The flora is a colorful one reminiscent of alpine regions of the North American Rockies. East of Mérida in the

Sierra de Santo Domingo the mountains are lower. The páramos are of similar rough aspect often surrounding glacial lakes but there may be shrubby vegetation in protected localities. Plants of J. canescens were widespread near the base of rocks and were conspicuously variable as to the size and indument of the pinnae. Some of them had many small, delicate, sterile leaves similar to those of Eriosorus. On the páramos and rocky ravines nearby there also occur Woodsia montevidensis (Spreng.) Hieron., Pityrogramma chrysoconia Desv., Cheilanthes marginata HBK. and species of Dryopteris, Asplenium and Athyrium. The largest colonies of Jamesonia observed were on the highest part of Páramo de la Negra in Táchira, Venezuela. There the plants form a carpet-like cover of white tomentose leaves in producing the

leaves in predominately grassy vegetation.

The floristically richest Colombian páramos were in the vicinity of Guasca and Páramo Palacio, north of Bogotá in Cundinamarca. J. rotundifolia and J. imbricata var. glutinosa were abundant in soil along the road cut and on the slopes above the road. There were also plants intermediate to these species and two species of Eriosorus growing among them. In patches of elfin-woods, the trees were covered with epiphytes including Polypodium cultratum Willd., Polypodium radicale Moritz, Polypodium rigescens Bory, and species of Trichomanes and Elaphoglossum and several small orchids. On the slopes above the road and in open soil along the road were Lycopodium attenuatum Spring, Lycopodium firmum Mett., Lycopodium Jussiaei Desv. and in high, flat areas Lycopodium rufescens Hook. occurred in Sphagnum. Several species of Paepalanthus were abundant and also Gentiana along with larger plants of Puya, Berberis, the ericaceous shrub Macleania and the arborescent Blechnum Buchtienii Rosenst. On a drier páramo, Patano Redondo, near Zipaquirá, which is known to be burned, we found J. robusta growing in a few large patches. It occurred also on an undisturbed hillside with outcropping sandstone to the east near Tausa, growing with J. bogotensis. In the Cordillera Central, on Páramo Ruiz, J. robusta also grew in drier, grassy areas and on the more moist road cuts there was J. Scammanae. On Ruiz there were some plants of Espeletia and Lupinus alopecuroides but the characteristic páramo vegetation has given way largely to grass through



Plate 2. Above, a plant of J. rotundifolia, Páramo de Puracé, 3250 m. Cauca. Colombia showing the densely tomentose, indeterminate apical buds of the leaves and stacked, sparsely indumented pinnae; below, leaves in a colony of J. canescens, Páramo near Laguna de Anteojos, 4000 m., above Mérida, Venezuela.

burning and pasturing. The soil profile along the road there consisted of alternate bands of black and light brown soils. The black type formed the top layer, of the present páramo, and contained a large portion of humus presumably formed through slow deterioration. Humus was less evident in the lighter brown layers and this was formed, at least in part, from volcanic tuff. The banding showed repeated fluctuations which have interrupted the darker formation of páramo soils.

On Volcan Puracé, in Cauca, J. Scammanae, J. imbricata var. glutinosa and J. rotundifolia (plate 2) grew in scattered colonies along the road cut and adjacent slopes and on an open, grassy site there was a large colony of J. pulchra. The higher, wet areas of the volcano were rich in species of Lycopodium, Begonia, orchids and bromeliads, and the Compositae, except for Espeletia, were less conspicuous than in other páramos.

It is sometimes difficult to determine accurately the altitudes at which collections of Jamesonia have been made for they are reported as general ranges covering several hundred meters. Plants occur largely between 3000 and 4000 meters; the lowest record I have is at 1500 m. for J. blepharum in southern Peru and the highest at 5000 m. for J. cinnamomea in Ecuador. The three species with the widest geographic ranges also have the broadest altitudinal distribution with J. Scammanae having the greatest from 1830-4300 m. J. brasiliensis has the lowest altitudinal range, 2300-2600 m. and J. cinnamomea has the highest 3100-5000 m.

There is some correlation in the degree of specialization of species and the altitude at which they occur. J. Cuatrecasasii and J. imbricata var. meridensis are specialized forms and are reported from above 3500 m. In the closely related group of J. verticalis, J. blepharum and J. cinnamomea, the latter is most specialized and occurs at the highest altitude. In other species this correlation is not found for the relatively unspecialized species J. rotundifolia and the more specialized one, J. canescens, occur at nearly the same altitude.

The most restricted area in which all species occur (the least common area, Map A) is between Mérida, Venezuela and La Paz, Bolivia. The area of greatest species concentra-

tion, where eleven of the twenty-one taxa occur is between

Bogotá, Colombia and Cuenca, Ecuador (Map A).

The geography of two groups in Jamesonia, distinguished on the basis of symmetry of the pinna and spore color, is considered separately. The first group of six taxa have symmetrical pinnae and dark spores. Among these J. verticalis. J. blepharum and J. cinnamomea form a distinct group. Each of these species occurs in the area of greatest species concentration, the first almost confined to it and the other two have widely disjunct stations extending south into Peru and Bolivia. Of the other three taxa, J. imbricata var. glutinosa occurs in the area of species concentration, J. scalaris and J. brasiliensis occur south of this in Peru and Bolivia. The last is the most notable member of the genus geographically because of its station on Mt. Itatiaia in Brazil. It was formerly considered to be endemic there but a few collections are now known from the highlands of central Bolivia. Eriosorus is also predominately Andean with a few species in Brazil. The latter are morphologically distinct from the Andean species except for E. elongatus which also occurs on Mt. Itatiaia and is widespread in Bolivia, Peru and Ecuador. The geographic history of this species seems to be similar to that of J. brasiliensis. A. C. Brade (1942) discussed the distribution of this along with other ferns having related species in the Andes. The disjunction between Brazil and Bolivia is noted in several fern genera by K. U. Kramer (1957) in his treatment of Lindsaea and he considers the possible connection through Matto Grosso and Minas Gerais. In a recent paper on the origin of the flora of southern Brazil, L. B. Smith (1962) takes up the Andean relationships in several genera of flowering plants. In Tillandsia usneoides, migration appears to have been from the Andes into southern Brazil and the same direction from the Andes into Brazil is evident in J. brasiliensis. There is, however, information from other groups that a westward migration has also occurred. This is discussed by R. Tryon (1944) in his study of the phytogeography of Doryopteris in which the species are concentrated in southeastern Brazil and migration is indicated westward into the Andes.

The species of Jamesonia having asymmetrical pinnae, and light brown or tan spores represent the largest group

including the widest ranging as well as the most restricted members of the genus. J. Alstonii has the widest distribution from Central Bolivia to southern Mexico. J. Scammanae and J. rotundifolia also occur in both South and Central America and all three of these species occur on the volcanos of Costa Rica. They most probably migrated there from Colombia before the main orogeny of the Andes during the middle and late Tertiary. The land bridge connecting Colombia with Nicaragua was available for these species from late Miocene and Pliocene times. K. U. Kramer (1957) proposes a northward migration in Lindsaea from the Choco region of Colombia to the volcanos of Costa Rica on the basis of the close relationship of Lindsaea Seemannii, endemic to to the Choco, and the Costa Rican endemic, L. pratensis. In the distribution of species in Eriosorus, Equisetum and Doryopteris there is also evidence for a northward migration. In other groups, however, as Pellaea (Tryon & Britton, 1958) there are cytological data which show that a southward migration from Mexico into South America has occurred.

The species in Jamesonia having the most restricted distributions are J. laxa, J. auriculata and J. canescens in the State of Mérida, Venezuela and J. Cuatrecasasii and J. imbricata var. meridensis which also occur there and with second stations in the sierras of northern Colombia. The first two are relatively unspecialized forms and the latter three are specialized.

If the relatively restricted and isolated areas in which the species now occur are considered along with the relatively broad geographic ranges of some of the species, the idea that the conditions under which the plants now grow were at one time more widespread is supported. During Pleistocene glaciation when glaciers descended to an average of 4000 meters in the Andes, the cold, moist conditions under which these species grow would have reached lower altitudes resulting in a greater continuity of this type of habitat.

The present ranges of the species afford some evidence for past distributions. From the least common area between La Paz, Bolivia and Mérida, Venezuela, species such as J. Alstonii, J. rotundifolia and J. Scammanae probably migrated north into Mexico and the last also south of the area into central Bolivia. Eleven species occur in the area

of concentration and it is possible that this may be a center of origin for some of them.

Some conclusions can also be drawn from the nine species which do not occur in the area of species concentration. Five of these are concentrated mainly in the Sierra Nevada de Mérida in Venezuela. Of these J. auriculata and J. laxa are most restricted and least specialized. They are species which have been either derived from an ancestor in Eriosorus in or near this region or perhaps represent isolated elements of once more widely ranging species. The others, J. Cuatrecasasii, J. canescens and J. imbricata var. meridensis, are more specialized taxa of Mérida which are related to species occurring southwest in Colombia. The three species that occur south of the area of species concentration, J. boliviensis, J. scalaris and J. brasiliensis, are morphologically distinct from the previous species and illustrate the development and migration of species in the southern and southeastern portion of the range.

MORPHOLOGY AND ANATOMY

RHIZOME. — The rhizome in Jamesonia is cylindrical, creeping, dichotomous and slender 0.5-5.0 mm., usually about 2 mm. in diameter (plate 3). Coarse roots, nearly equal to the petioles in diameter, arise in the stele and protrude from any surface. These are often dense and matted about the rhizome and are especially large adjacent to the petioles. There is a collar of epidermal tissue ensheathing the root where it emerges from the rhizome. The leaves are alternate and variously distant on the rhizome depending upon the compactness of the axis. A leaf gap occurs above the leaf trace, or if the internodes are shortened, the leaf gaps may overlap and the stele is correspondingly dissected. The rhizome is an amphiphloic siphonostele having dictyostelic stages. There is a central sclerotic pith and a neck of similar tissue connected to it where the stelar ring is interrupted by leaf gaps. The vascular tissues of the root are contiguous with those of the rhizome and with the exception of the endodermis are unbroken where these organs join.

The rhizome is composed of an epidermis, more or less covered by trichomes, cortex, and stele with a central pith which consists of thick walled cells. The epidermis consists of small, brown, thin walled cells which form a rather even



PLATE 3. Plants of J. canescens from Páramo de la Negra, 3000 m. Táchira, Venezuela showing the elongate creeping rhizome. Plants from this páramo have especially dense, whitish tomentum on the leaves. Tryon & Tryon 5886 (GH).

surface. The trichomes arise from the epidermis and consist of larger, inflated cells and are usually darker colored. The cortex is composed largely of sclereids having thick, dark brown walls with slit-like pits and large lumina usually filled with spheroidal starch particles. The pith and cortex as well as the neck of tissue which connect these at the leaf gaps are of this same sclerotic tissue. There is an area of parenchyma tissue in the cortex adjacent to the outer endodermis which is unusual in fern rhizomes. This tissue completely surrounds the stelar ring or is adjacent to the outer layer of endodermis if the stele is dissected, and is also filled with starch particles. The stele has an internal and external layer of relatively small, brown-colored endodermal cells. There are thin walled cells, clear or scarcely colored, within the endodermal tissues which form the pericycle or possibly portions of the phloem. These are larger and less compressed than the adjacent angular cells of the phloem which are often crushed in transverse section. The xylem is composed of compact tracheids of various sizes having acute ends and scalariform to somewhat reticulate thickened cell walls. The amphiphloic stelar arrangement in Jamesonia occurs in several other genera with creeping rhizomes as Adiantum and Dennstaedtia. The dissected form of the stele, with overlapping leaf gaps resembles the form of some stages of the rhizome of Anemia phyllitidis. The rhizome of Jamesonia represents an intermediate type having both siphonostelic and dictyostelic stages and with fewer changes in form than rhizomes of Anemia or Schizaea.

The dermal appendages of the rhizome are concolorous, tan to lustrous black and range from 0.5-3.0 mm. long. For the whole or most of the length they are one cell wide although the basal cell may be larger and inflated and the attachment to the epidermis of the rhizome may be in the central rather than the basal portion of this cell. In several species there are two or more cells at or near the base and in the strict sense these appndages would not be trichomes but neither are they scales for they are thickened with clustered cells. The rhizomes in all species of Jamesonia have some trichomes only one cell wide and in some species only this kind occurs, thus I consider the more elaborate appendages, having more than one cell at the base, as modified or bristle-like trichomes. Light colored trichomes, only

one cell wide, are usually lax and patent and darker ones, a few cells broad at the base, are usually rigid and appressed to the rhizome. The terminal cell of the trichome is usually acuminate as in J. canescens and J. Scammanae and similar to other cells of the trichome. In some species the terminal cell is bulbous, of a clear diaphanous material, and appears as if the outer portion of the cell wall has been cast off. In J. Alstonii, J. verticalis and J. imbricata var. glutinosa these occur on the older portions of the rhizome and the acuminate form nearer the apex. In J. scalaris, J. brasiliensis and J. Goudotii the rhizome trichomes are predominately of the bulbous form and in J. blepharum and J. verticalis an exudate is produced at the bulbous apex. In some species of Jamesonia the rhizome indument is relatively uniform, correlates with other characters and expresses relationships, but for the most part it is more plastic than other characters of the plants. In Eriosorus and Pterozonium the rhizome indument is of the same form, with the same variations as in Jamesonia, and may be useful in establishing natural lines between these genera. The rhizome indument is also similar in other gymnogrammoid genera Syngramma, Craspedodictyum, Taenitis and Aspleniopsis but if a relationship exists between these genera and Jamesonia it is more distant.

LEAVES AND PINNAE. - Most species of Jamesonia have leaves with indeterminate growth. This is evident in the continued development of the apical bud while the basal pinnae on the leaf have deteriorated or been lost. In J. laxa the pinnae are in marked growth zones. The leaf apex is usually fully expanded and determinate in J. verticalis and sometimes so in J. cinnamomea, J. blepharum and J. imbricata var. glutinosa. In seven of the species there are specimens in which the basal pinnae are thin textured, plane and with dentate margins and in these characters are distinct from the upper pinnae. There may be several small leaves wholly of this form and resembling those of Eriosorus. The leaf form in Jamesonia, although generally more reduced in most species, resembles that in Eriosorus, particularly Eriosorus elongatus. The leaves in this species may be bipinnate, pinnate-pinnatifid or once pinnate and slightly lobed. The generic separation between Eriosorus and Jamesonia on the division of the lamina breaks down with this material.

129

In Eriosorus diversity of leaf form is less notable than in larger genera as Adiantum or Lindsaea since its closest relatives have been segregated mainly on leaf division. The leaves in most species of Eriosorus are small - less than 30 cm. long, bi- or tripinnate and are broadest at the base. The most reduced form is Gymnogramma longipetiolata (this has not been transferred to Eriosorus) which has few, entire pinnae at the end of a long petiole. There is a group of species related to Eriosorus flexuosus, with scandent leaves which may be a few meters long and elaborately branched in several planes. In Eriosorus and related genera, generally, species with leaves more than once pinnate are treated in Eriosorus, those with entire, simple leaves are in Pterozonium - although in these the sori are also specialized - and those with once pinnate, linear leaves are included in Jamesonia. Generic separation of this kind based solely on leaf form is incongruous for in Eriosorus elongatus, Pterozonium spectabile as well as in Jamesonia the leaves are once pinnate and linear. The greatest diversity in leaf form occurs in Eriosorus and it is possible that the types found in related genera may have been derived from this source.

In Jamesonia there are specific differences in the form of the pinnae, the orientation of the stalk and especially in the elaboration of the margin. The contracted pinna form of most species is indicative of a reduced condition but in two species the pinnae are relatively elongate. In one of these, J. auriculata, the basal lobes of the pinnae are comparable in size and form to the whole pinnae in other species. In J. canescens the acroscopic lobe is bent or the whole pinna is twisted and in J. bogotensis one or both of the basal lobes project above the upper surface of the pinna. These species with bent or twisted pinnae are considered more specialized than J. robusta in which the pinnae are accommodated in one plane. Two closely related species J. Alstonii and J. Goudotii differ in pinna shape. In the former they are mostly orbicular or ovate and in J. Goudotii, which is more specialized in other characters, they are mostly reniform. The pinnae in J. scalaris are usually three lobed and they are sometimes irregularly lobed in J. Scammanae. J. imbricata var. glutinosa and J. brasiliensis have symmetrical pinnae with the bases incurved and truncate.

There are three types of modification of the pinnae stalks each of which seems to reflect an independent change toward the reduction of the lamina. In J. verticalis the pinnae stalks are broad or the pinnae adnate and J. blepharum and J. cinnamomea with shorter pinnae have longer pinna stalks. The stalks in J. imbricata var. glutinosa, J. brasiliensis and J. pulchra are strongly bent and in the latter they may be curved nearly 90° and overlay an enlarged pinna lobe. The stalks are attached to the upper pinna surface and easily articulate in J. Cuatrecasasii. They also freely articulate in J. peruviana and J. scalaris. They are sometimes glandular as in J. bogotensis. The stalk color is atropurpureus or brownish and is carried into the veins of the pinnae in J. auriculata, J. laxa and J. rotundifolia. In other species as J. canescens and J. Goudotii the dark color extends only part way into the stalk and the upper portion and the veins of the pinna are tan.

The form of the pinna margin is one of the most useful diagnostic characters although this must be examined at approximately 80 magnifications. There is usually a border of specialized cells several cells broad along the margin which differ in texture from the rest of the pinna. In some species, particularly *J. imbricata* var. *glutinosa*, there is much variation in the border but for the most part it is one of the most useful characters for identification of the species and for establishing their relationships.

In the related species J. auriculata, J. laxa and J. rotundifolia, the margins are similar to those in many species of Eriosorus with few, irregular, protruding cells although in the latter a rather broad border may be developed. Other species close to these with tomentum on the lower surface have broad, membranous, dentate borders which may be indusioid. The less tomentose species related to J. verticalis have entire margins with cilia especially abundant at the vein ends.

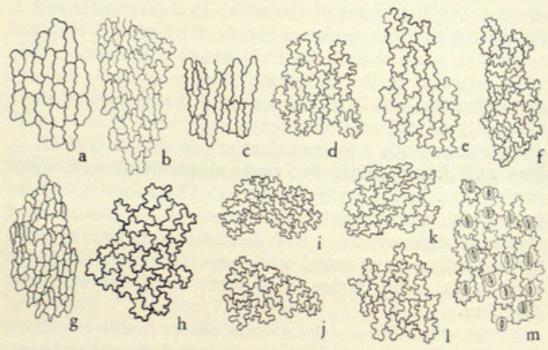
Venation of the pinnae is open dichotomous. There may be characteristic patterns in groups of species but there is considerable variation depending upon size and shape of the pinnae. The position of the veins in the pinna tissues is usually near the upper surface or slightly sunken but in a few species they are raised. There are differences in the width and length of the veins, the angle at which the branch-

es part and the shape of the ends. In *J. verticalis* and *J. blepharum* the vein angles are acute, the branches long and somewhat parallel and the ends broad and cuneate. The veins adjacent to the rachis are short and broad, the ultimate branches are long and equally dichotomous and there is usually no differentiated central member. They are also dichotomous with long ramifications in *J. rotundifolia*, *J. laxa* and *J. auriculata* but more slender and with wider angles than in the previous species. The venation is sympodial with a prominent central vein in *J. auriculata*. Most species particularly those with dense tomentum on the lower pinna surface have broad veins especially near the pinna stalk with wide angles and short to moderately long branches.

strongly undulate walls and are generally longer than broad. Near the veins they are rather rectangular and less undulate and near the pinna margin they are smaller with deeply undulate walls. In some species as J. canescens and J. Alstonii the epidermal cells are more uniform than in others. In J. rotundifolia and J. canescens the upper epidermal cells are about twice as long as they are in J. Scammanae, J. imbricata var. glutinosa and J. scalaris. The size of the cells is not correlated with the pinna size for a pinna of J. scalaris, about a third the size of one of J. imbricata var. glutinosa, may have epidermal cells as large as or larger than those of the latter.

The thick cell walls which occur in J. Alstonii and J. Goudotii are apparent in the dried condition. A distinct pattern of epidermal cells in J. verticalis and J. auriculata with nearly rectangular cells having slightly undulating walls is similar to that in species of Eriosorus.

The lower epidermis is distinguished from the upper by the stomata and smaller U-shaped cells with deeply undulate walls surrounding the guard cells. The pattern of the cell walls of the lower epidermis is relatively constant in all of the species although there are differences in the size of the guard cells. It would be of interest to survey larger samples to determine if these size differences might reflect different polyploid levels. The pattern of epidermal cells in most species of Jamesonia is illustrated by the series (d-f and h-l), and another form by (c and g) and also those of two



Epidermal cells from the mid-portion of the pinnae, equidistant from the veins: a-1 upper epidermis, m. lower epidermis, all × 45. a, Gymnogramma Mathewsii, Tryon & Tryon 5958 (gH); b, Eriosorus elongatus, Killip & Smith 23249 (gH); c, Jamesonia auriculata, Alston 7050 (gH); d, J. rotundifolia, Cuatrecasas 20223 (gH); e, J. canescens, Gabaldon, in 1922 (US); f, J. boliviensis, Vargas 1060a (gH); g, J. verticalis, Cuatrecasas 8793 (US); h, J. Goudotii, Cuatrecasas 19110 (gH); i, J. scalaris, Bües 2163 (US); j, J. peruviana, Macbride & Featherstone 1883 (gH); k, J. imbricata var. meridensis, Tryon & Tryon 5801 (gH); l, J. imbricata var. glutinosa, Idrobo et al. 3150 (gH); m, J. imbricata var. glutinosa, lower epidermal cells and stomata, Idrobo et al. 3150 (gH).

species of Eriosorus (a and b), illustrate the distinct patterns.

PETIOLE. — The petioles are castaneous to atropurpureous or sometimes blackish and usually strongly bent and appressed to the rhizome for a short distance before ascending. In most species they are shorter than the rachis but they may be up to four times longer in J. verticalis. The petiole thickness has in the past been reported in comparison to the thickness of the quills of various bird feathers. Both length and diameter of the petiole may vary in the species depending upon the habitat of the plant. Those from grassy or mossy sites where the rhizomes are deeply embedded in the vegetation have longer more delicate, filiform petioles than those growing higher among rocks. In species with filiform petioles they are thinnest just above the rhizome. The thickest petioles, about 3 mm. in diameter throughout, occur in J. cinnamomea. Petioles are terete, oval, or slightly flattened or channeled on the upper surface.

At 1 cm. above the rhizome the tissues are arranged sim-

ilarly to those of the rachis. The epidermis is composed of dark brown cells and the cortex of thick walled, brown cells comprises the largest portion of the petiole. The cells of the cortical sclerenchyma are smaller adjacent to the epidermis and at the open side of the vascular arc. The endodermis surrounds the vascular tissues and as in the rhizome some parenchyma tissue occurs in the adjacent cortex. These cells and the adjacent sclerotic cells contain numerous, spherical starch particles. The vascular tissues form a central flattened U-shaped or C-shaped arc open at the upper surface of the petiole. The xylem consists mostly of large tracheids with smaller elements at the ends and sometimes at the center. The tracheid walls have scalariform or helical thickening. Adjacent to the xylem on the open side of the arc there are some angular and thin walled, homogeneous cells which may be phloem and possibly pericycle.

The indument on the petioles is less dense than on the rachis and is often lost with age but the form of the trichomes is similar to that of the rachis. The basal cell is often contracted into a foot-like portion as in the rachis trichomes.

RACHIS. — The rachis is generally the same color as the petiole or slightly lighter. The shape of the transverse section in the basal third of the lamina is terete to ellipsoidal or triangular with the lower surface convex and the upper surface of two planes converging in a broad angle or in a few species the rachis is channeled. The pinnae are decurrent on the rachis in *J. verticalis* and slightly so in some specimens of *J. Goudotii*. The pinna stalks in most species depart abruptly from the upper surface of the rachis nearly at right angles to it, and the pinnae are slightly imbricate to compactly stacked. In *J. brasiliensis*, *J. Scammanae*, *J. cinnamomea* and *J. imbricata* var. glutinosa the pinnae may overlay the upper surface of the rachis.

The rachis is composed of the outer epidermal tissue consisting of small dark brown walled cells from which project one to several trichomes. The cortical cells adjacent to the epidermis are smaller and thicker walled than those near the vascular tissue. The vascular trace is surrounded by a ring of brown-colored endodermal cells. In the central portion of the trace there is a V-shaped or U-shaped arc of xylem open toward the upper surface of the rachis with extended ends

perpendicular to the main figure. The cells are mainly large metaxylem cells and smaller protoxylem at the bottom and ends of the figure. The pinna traces depart at the ends of the arc. There are homogeneous patches of thin, angular cells which appear to be phloem at the ends of the arc and also in the center. Between these and the endodermis there are thicker walled cells, somewhat longer than broad and often crushed, which appear to be pericycle.

The rachis indument is similar to that of the petiole but denser and sometimes more elaborate. The trichomes are one rowed, multicellular with dark joints between cells. The cells are diaphanous, tan or ruddy brown and the upper ones sometimes darker. When dry the cells are twisted near the joints and alternately aligned in a catenate arrangement. The basal cell of the trichome is usually inflated and may have a constricted, foot-like portion attached to the epidermis. The apical cell of the trichome is long and acuminate or short and bulbous and one type is usually constant for the species although in some, both of these forms may occur on one leaf. In J. Scammanae and J. imbricata var. glutinosa there are glands on the rachis similar to those on the upper surface of the pinnae and these produce a crustose substance on the rachis.

SPORANGIA. - Sporangia may be borne along the veins from the pinna stalk to the distal portion of the veins but not terminally. In J. laxa and J. brasiliensis there are usually few sporangia located in the central portion of the pinna near the stalk. They are usually abundant in J. Alstonii and J. Goudotii and obscure the entire lower pinna surface and extend under the enrolled margins. The sporangia of Jamesonia have been described by Thompson and Bower as acrostichoid with some of them borne on the tissue adjacent to the veins. I have examined the species in which they report this condition, particularly J. verticalis, and have found that the sporangia are attached only on the veins although the capsules may cover the tissue between veins. In species with relatively large pinnae as J. verticalis and J. auriculata a progressive sequence can be seen in the maturity of the sporangia from the central portion of the pinnae toward the margins. In Jamesonia and also in Eriosorus sporangia develop in a acropetal sequence. In some material a few

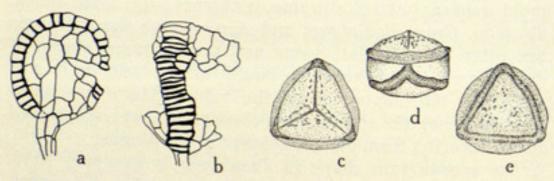
Trichomes occur among the sporangia in some species and these are similar to those on other parts of the pinnae. The position and sequence of maturity of the sporangia in Jamesonia and Eriosorus differ from those of other gymnogrammoid genera having rhizome trichomes. In Syngramma, Taenitis, Craspedodictyum and Aspleniopsis the sporangia are often on reticulate veins and are in mixed stages of development throughout the length of the vein or in sori variously interrupted along the veins. There are paraphyses, among the sporangia in these genera, of a specialized form, differing from other indument of the pinnae.

The sporangium shape in *Jamesonia* is generally pyriform, somewhat longer than broad or orbicular. The annulus is more or less oblique and interrupted by the stalk. The sporangium stalk is usually short, about one fourth the capsule length and usually of 2 or 3 tiers of cells. There are 3 cells adjacent to the capsule and there also appear to be 3 cells at the base. The stalk may be extended by the elongation of cells or increase in number by intercalary divisions. Cell division occurs in the lower portion of the stalk and may result in a cushion of cells subtending the capsule. The cushion is sometimes dark brown and with one or more trichomes.

The annulus is considered here as the uninterrupted series of indurated cells. The shape and position of the cells may be irregular or rarely the annulus is absent but it is usually a sequence of about 20, yellow or amber-colored cells approximately one fourth or one third the width of the capsule. The number of annular cells was considered by earlier workers to be characteristic of the species but variation seems to be greater than was realized. The greatest number, 33, is in J. robusta and the fewest, 12, is in J. brasiliensis but the number ranges between 15-25 in most species. The stomial region below the annulus consists of 2-4 small, thin walled cells followed by 2-5 indurated cells between which the sporangium usually opens. There are about 3-5 thin walled cells between the indurated ones of the stomium and the stalk. The capsule faces are unequal in size and can be distinguished by 2 rows of cells leading from the stalk to one face and a single row leading to the other face. The cells of the capsule face are generally angular and usually smaller and

more numerous than those in the sporangia of Polypodium and Vittaria illustrated by Wilson (1959).

spores. — Spores were examined in the dried condition, in lactic acid preparations and in a few species material was prepared by acetolysis and mounted in glycerine. Observa-



Sporangia and spores. Sporangia: a, J. cinnamomea, lateral face, × 55, Sodiro 9/900 (US); b, J. canescens, showing irregular cells in the annulus, × 55, Tryon & Tryon 5832 (GH). Spores: J. canescens, c, proximal face showing the three angles darkened, not projecting beyond the equatorial wing in this species; d, lateral view, the darkest shading indicating a portion of the triangular ridge on the distal face; e, distal face with triangular ridge and slightly verrucose, Tryon & Tryon 5826 (GH).

tions of the spores were made under 125 and approximately 600 magnifications with apochromat objectives and compensating oculars. A spore identified as one of Jamesonia imbricata is included in the series of illustrations published by Erdtman (1957), and represents the general form for the genus. The spores of Jamesonia are similar to those of Eriosorus and Pterozonium and are of a form quite distinct from other gymnogrammoid ferns. In Jamesonia, spore color ranges from tan or straw to amber color or medium to dark, ruddy brown and is fairly constant within species. There are two fairly distinct groups based on spore color and symmetry of the pinnae. In J. verticalis, J. blepharum, J. cinnamomea and J. scalaris, J. brasiliensis and J. imbricata var. glutinosa, the pinnae are symmetrical and the spores are dark, ruddy brown (with the exception of a collection of J. blepharum, north of Bogotá). In the other species the pinnae are asymmetrical and the spores light colored from tan to medium brown (with the exception of J. robusta which usually has dark brown spores). Spore shape is tetrahedral, with three meridional planes which are contact planes in the tetrad, and a free convex surface which is greater than a half sphere. In polar view the three meridional or radial planes with the trilete dehiscence fissure is designated the proximal face and the rounded one the

distal face. The spore outline in proximal view is sub-triangular with three convex sides and three more or less protruding angles. An equatorial ridge or wing, which may be lobed, divides the faces unequally. There is no perispore and the sculpture described is that of the exine. On the proximal face there is usually a lip or sculptured band parallel to the triradiate scars. The three planes are smooth, papillose to verrucose or slightly rugose. On the distal face there are three contiguous ridges forming a triangle. This serves as a base upon which the spore usually rests, thus the distal face is less often apparent. The angles of the triangle are usually connected by short ridges which join with and may project beyond the equatorial wing. The surface within the triangle on the distal face is smooth or more or less papillose to verrucose and may be more prominently sculptured than the proximal face.

The number of spores in an unopened sporangium is between 59 and 64 and the latter is considered a full complement. Thompson (1918) reports the number for Jamesonia to be 56-72 and considers this to be a basis for placing the genus between the gradate ferns and the simplices. I have not found more than 64 spores in a sporangium in any of the material I have examined and I have particularly surveyed the species J. cinnamomea and J. verticalis he mentions and the collection of J. scalaris that he cites from Peru. Irregularly developed spores are frequent in the material I have examined of J. laxa and J. pulchra. An unusual specimen of J. Goudotii from southern Colombia appears to be a hybrid and in this the spores are exceptional-

ly large and irregular.

CHROMOSOME NUMBER. — A chromosome number for the genus was obtained in J. bogotensis from sporangia fixed in glacial acetic acid and alcohol. The spore mother cells were prepared by the aceto-carmine squash method. The collection is from Páramo de Chisaca, south of Bogotá, at 3400 m. made on October 27, 1961 (Rolla M. and Alice Tryon 6178, GH). Most of the cytological preparations of Jamesonia, fixed in three parts alcohol to one part glacial acetic acid were deteriorated a month after they were fixed and it was only the most recently collected material that yielded results. The report is a tentative one, based upon the analysis of two cells with n = 87, (plate 4). These were in polar view of

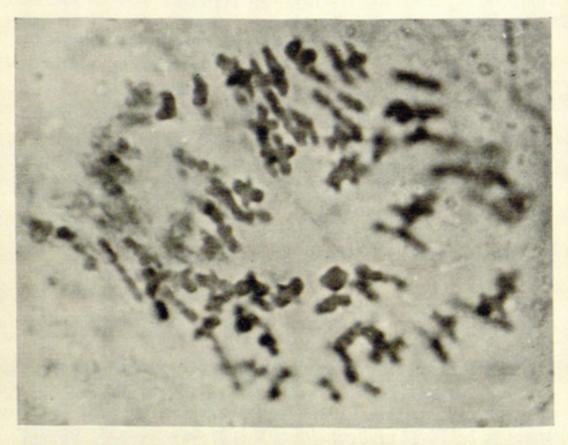


PLATE 4. Above, chromosomes of J, bogotensis, polar view, late Metaphase I in meiotic division (n=87), about \times 2000. Tryon & Tryon 6178 (GH); below, explanatory diagram for photograph. The broken lines indicate three bivalents which are partly covered by overlaying ones.



late Metaphase I in meiotic division with nearly all of the chromosomes as bivalents and with no trivalents. Some of the chromosomes showed early Anaphase separation with a connecting strand of chromatic material. The number n = 87 is thought to be a hexaploid on the base of 29. Preliminary as this report may be, it is of particular interest, indicating that hybridization probably occurs in the genus and that morphological intermediates may be of hybrid origin. It also suggests the possibility that there exist, or have existed, other members at diploid, triploid and tetraploid levels from which the hexaploid might be derived. Some morphological intermediates occur where J. bogotensis and J. imbricata var. glutinosa grow together and should these be hybrids they would demonstrate further evolutionary potential from the hexaploid.

The report is also of interest in relation to the numbers reported by Manton (1958) for other gymnogrammoid genera — Syngramma n = 116 and Taenitis n = 44. In the correlation she draws between chromosome number and position of the genera in the Pteridaceae of Copeland, Jamesonia would be an exception of the same kind as Syngramma and out of place among the genera in Copeland's scheme.

On the basis of chromosome numbers in the series of 29, Jamesonia can be placed with genera as Anogramma, Onychium, Pellaea, Cheilanthes and Pteris. In these genera polyploidy is also a mechanism of evolutionary significance.

PREPARATIONS. — Descriptions and drawings of the pinnae were prepared from material cleared in sodium hydroxide. Measurements are from dried material with the exception of the trichomes which were made from preparations fixed in lactic acid. All of the outline drawings and those of cellular detail have been traced from specimens projected on a Bausch and Lomb Microprojector. I am most appreciative of the careful inking of these tracings by Mrs. Joyce Todd. The drawings of the spores were prepared by Mrs. Ruth Hsu Chen and I am grateful to her for the careful attention to detail and shading of these.

The maps of the distributions have been plotted on the Goode series of base maps, published by the University of Chicago Press.

SYSTEMATIC TREATMENT

Jamesonia Hook. & Grev. Icon. Fil. 2: t. 178. 1830

Gymnogramma, Section Jamesonia (Hook. & Grev.) Kl. Linnaea 20: 407. 1847.

Psilogramme, Section Jamesonia (Hook. & Grev.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 332. 1882.

Rhizome slender, long or moderately long creeping, siphonostelic with dictyostelic stages, densely clothed with tan to black, patent or appressed, bristle-like trichomes of 1-5 cells at or near the base. Leaves linear, usually 15-60 cm. long, seldom exceeding 90 cm. long, less than 5 cm. broad, indeterminate or sometimes determinate, once pinnate or rarely pinnatisect. Petiole and rachis channeled, terete or trigonous with the upper surface obtusely angled, tomentose, more densely so on the lower surface or glandular. Pinnae small, usually not exceeding 1 cm. in either length or breadth, mostly imbricate in 2 ranks laterally disposed or overlaying the rachis, more or less orbicular, ovate-cordate or long-ovate, seldom auriculate or lobed, herbaceous or coriaceous, more or less tomentose, especially the lower surface, or glandular, with margins incurved or enrolled having a membranous, entire, dentate and/or ciliate border. Veins free, dichotomous, the branches unequal. Sporangia on the veins in the basal portion of the pinna or crowded, extending to the distal portions and obscuring the lower surface of the pinna; sometimes immersed in tomentum on the lower pinna surface but without paraphyses, the stalks short to slightly longer than the capsule, 3 cells broad, often with intercalary cell divisions, the annulus interrupted by the stalk, of 12-33, usually 20 indurated cells. Spores tetrahedral-globose with trilete commissural ridges and 3 more or less projecting angles, with a prominent equatorial wing, the distal face with 3 ridges forming a triangle, exine smooth or more or less verrucose.

TYPE SPECIES: Jamesonia pulchra Hook. & Grev.

USE OF THE KEY

Macroscopic characters have been used in the key where possible but there are some rather critical characters which are obscure. Thus it is strongly recommended that the specimens be examined with up to 80 magnifications. This is especially important for observation of the pinna margin and indument. The latter is best observed on the younger pinnae near the lamina apex and with special care to distinguish between bulbous glands and the bases of broken trichomes. To observe the characters of the pinna, particularly the symmetry of the base, the stalk and the margin, it is usually necessary to make wet preparations of the material. Some specimens which are intermediates or peculiar variants may not agree with all of the characters under one heading. These are best identified on the totality of their characters rather than by any single one.

FACTITIOUS KEY TO THE SPECIES AND VARIETIES OF JAMESONIA

a. Apex of the petiole and base of rachis rounded or obtusely angled on the upper surface; pinnae in the central portion of the lamina

with more or less terete, long to rarely short, stalks
b. Pinna stalk attached in the sinus between the upper and lower
surfaces of the pinna.
c. Fertile pinna auriculate or lobed in the apical half of the lamina.
d. Pinnae coriaceous, cell walls of the upper epidermis thickened
and raised (visible at 10 magnifications) 12. J. Goudotii.
d. Pinnae herbaceous, cell walls of the upper epidermis not notably thickened or raised
e. Central pinnae of the lamina 2 or more times longer than broad,
up to 12 mm, long; upper surface of the pinnae pubescent,
2. J. auriculata.
e. Central pinnae of the lamina about as long as broad, up to 4
mm. long; upper surface of the pinnae glandular f f. Apical bud of the lamina vermiform, glutinose, with appressed
trichomes; pinnae in the central portion of the lamina short
stalked: pinna border entire or nearly so 9. J. Scammanae.
f. Apical bud of the lamina not vermiform or glutinose, with
patent to slightly appressed trichomes; pinnae in the central
portion of the lamina long stalked; pinna border ciliate
c. Fertile pinnae entire in the apical half of the lamina, rarely lobed
in species 5
g. Pinnae inequilateral at the base; spores tan to light brown, or
usually dark brown in species 5
h. Lower surface of the pinnae densely pubescent to tomentose, with crispate or loosely curled trichomes
i. Pinnae glabrous to conspicuously pubescent on the upper sur-
£]
i Pinna margins plane to incurved, with narrow borders which
are elaborated at the vein ends and not, or scarcely conti-
i Pinna margins enrolled, sometimes tightly so, with usually
broad borders which are contiguous, dentate, or entire,
b Dinne aspecially the older ones, convex on the upper sur-
face (natelliform) . the borders often narrow, irregularly
dentate
borders broad sometimes indusioid, entire or hearly so of
negative dentate
1 Dinnes stelle usually strongly bent and overlaying an
onlawed basel lobe of the ninna: pinnae orbicular of ovace
cordate
tanal manalit orbigular or lobed.
Dhisana trichomes lay natent, tan or nght brown,
tinht - then the whiteome surface: Ecuation and Colombia
nghter than the rinzome sarray, 5. J. robusta.

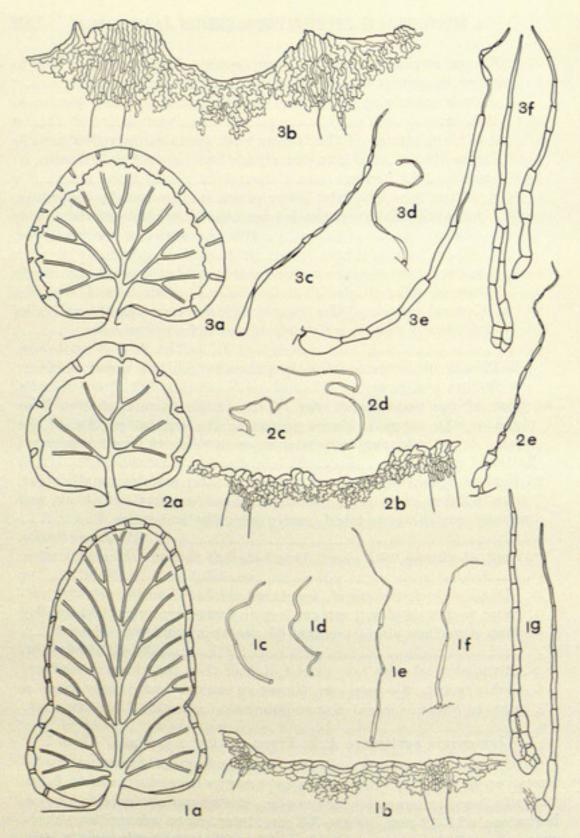
m. Rhizome trichomes rigid, appressed, dark brown or black- ish, darker than the rhizome surface; Venezuela
i. Pinnae glandular on the upper surface rarely also with a few trichomes.
n. Apical bud as broad as, or broader than, the expanded lamina, with patent trichomes; pinna stalks 1 mm. or more long.
o. Rhizome trichomes lax, patent, tan or light brown, lighter than the rhizome surface; pinnae orbicular to ovate; Peru, Ecuador and Colombia. p. Upper surface of the pinnae with one or both basal lobes raised above the plane of the pinna, usually with numerous glands and sometimes also crustose or with a few tri-
chomes; central and northern Colombia 7. J. bogotensis. p. Upper surface of the pinnae with both basal lobes in the same plane as the pinna, or directed downward from it, with few glands; Peru, Ecuador and southern Colombia 15A. J. imbricata var. imbricata.
 Rhizome trichomes rigid, appressed, dark brown to blackish, darker than the rhizome surface; pinnae ovate to usually long-ovate; Venezuela and Magdalena, Colombia.
n. Apical bud smaller than the expanded lamina (vermiform), with appressed trichomes; pinna stalks less than 1 mm. long.
9. J. Scammanae. 1. Lower surface of the pinnae glabrous, or sparsely pubescent with short, rigid trichomes along the veins, usually with a tuft of trichomes on the pinna stalk and basal veins
q. Upper pinna surface glabrous, glandular or with short, erect capitate trichomes or few longer ones
broader than long

- g. Pinnae equilateral at the base; spores dark brown, or tan to amber in species 9 and 15. t t. Pinnae glandular or crustose on the upper surface; Mexico to Bolivia, u Central pinnae of the lamina with conspicuous stalks usually more than 1 mm. long, sometimes bent; spores dark brown, or rarely light brown. v v. Pinna base truncate; lower pinna surface usually tomentose, to rarely glabrous, the border usually broad, dentate and/or ciliate. 15B. J. imbricata var. glutinosa. v. Pinna base cordate; lower pinna surface glandular or with a few, short trichomes, the border narrow, usually of a single row of cells, ciliate. 14. J. scalaris. u. Central pinnae of the lamina with short, inconspicuous stalks less than 1 mm, long; spores tan or light amber color, 9, J. Scammanae. t. Pinnae glabrous to slightly pubescent on the upper surface; Bolivia and Brazil. 16. J. brasiliensis. a. Apex of the petiole and base of the rachis sulcate, channeled or plane on the upper surface; pinnae in the central portion of the lamina broadly to narrowly adnate, or with short broad, somewhat flattened stalks. w w. Central pinnae broadly to narrowly adnate; petioles usually stout, usually 2 mm. or more in diameter; pinnae long-ovate to oblong and usually auriculate or lobed, rarely orbicular and entire. w. Central pinnae with short, broad stalks; pinnae orbicular, entire. x x. Rhizome trichomes rigid, appressed, darker than the rhizome surface; rachis slender, 1 mm. or less, in diameter; apical bud smaller than a mature pinna; central pinnae approximate to distant. x. Rhizome trichomes lax, patent, lighter than the rhizome surface; rachis stout, 2-4 mm. in diameter; apical bud larger than a mature pinna; central pinnae imbricate. 19. J. cinnamomea.
 - 1. Jamesonia auriculata A. F. Tryon, sp. nov. Fig. 1. Map 1

Trichomata rhizomatis patentia vel appressa castanea vel rufofusca, apex laminae indeterminatus gemmae tomento patente fulvo vel rufo-fusco, pinnae elongato-ovatae, plerumque auriculatae planae herbaceae ad 5-12 mm. longae 3-6 mm. latae, pinna adaxialiter pubescens, abaxialiter tomentosa trichomatibus fulvis crispatis, nervis latis prope petiolulum supra gracilioribus, dichotomis angulis modice latis, limbo angusto, brevilobato, latiore ad terminos nervorum, sporae fulvae vel pallide fuscae laeves.

TYPUS: Venezuela, State of Mérida, Páramo de la Negra, above La Canada, 2800 m. Feb. 14, 1939. A. H. G. Alston 7050, GH; isotypus,

Rhizome long creeping, dichotomously branched, ca. 2-4 mm. in diameter with moderately dense, coarse roots, the internodes variable



Figs. 1-3. Fig. 1. J. auriculata: a, pinna, × 5; b, pinna margin with two vein ends. × 35; c, trichome from upper pinna surface, × 30; d, trichome from lower pinna surface, × 30; e, rachis trichome, × 30; f, petiole trichome, × 30; all from Alston 7050 (GH); g, rhizome trichomes, × 30, from Stevermark 56291 (GH). Fig. 2. J. laxa: a, pinna, × 10; b, pinna margin with two vein ends, × 35; c, trichome from upper pinna surface, × 30; d, trichome from lower pinna surface, × 30; e, rachis trichome, × 30; all from Funck & Schlim 1118 (LE). Fig. 3. J. rotundifolia: a, pinna, × 5, from Cuatrecasus 20223 (GH); b, pinna margin with two vein ends, × 35, from Scamman & Holdridge 7928 (GH); c, trichome from upper pinna surface, × 30; d, trichome from lower pinna surface, × 30; e, rachis trichome, × 30; the last three from Alston 7232 (GH); f, rhizome trichomes, × 30, from Alston 7459 (US).

in length, the trichomes rigid, appressed, castaneus or ruddy brown, slightly darker and more ruddy than the rhizome surface, 2.0-2.5 mm. long with usually 1 (-3) cells at the base, apex acuminate. Petiole strongly bent and somewhat appressed to the rhizome before ascending, 4.5-10.0 cm. long, 1/8-1/6 as long as the lamina, castaneus or atropurpureus, terete, ca. 1.0 mm. in diameter at the apex slightly more slender below, more or less pubescent, the trichomes similar to those of the rachis. Lamina once pinnate, 14-60 cm. long ca. 0.5-2.0 cm. wide, broadest in the central or upper portion (not at the apex) narrowed toward the base, with ca. 50-150 pinnae, indeterminate, the apical bud smaller than the mature pinnae, with trichomes matted or patent. Rachis atropurpureus usually the same color as the petiole or darker, terete, ellipsoidal, or trigonous and the upper surface with an obtuse angle, with dense matted pubescence, the trichomes not exceeding the length of the pinnae, somewhat longer on the lower surface adjacent to the pinnae, tan to rust colored, with the cells near the base sometimes clear, the apical cell acuminate. Pinnae alternate or subopposite in 2 ranks laterally disposed, imbricate or distant, (the basal ones usually smaller, distant, sterile, finally deciduous, sometimes flat and strongly dentate) long-ovate, usually auriculate, plane with the margin more or less enrolled, inequilateral at the base, 5-12 mm. long, 3-6 mm. wide, light green, herbaceous; upper surface pubescent with tan or gold colored trichomes, the epidermal cell walls unth'ckened; lower surface tomentose with tan, crispate trichomes of few long cells; stalk straight or oblique and slightly bent, ca. 0.5 to nearly 1.0 mm. long, the dark color of the stalk extending into the adjacent veins of the lower pinna surface. Veins broad, especially near the base, and more or less sunken, dichotomous, the angles wide, with moderately long branches, the ends clavate or flabellate, extending to the margin. Border narrow, shallowly lobed or slightly extended at the vein ends, clear or opaque white. Sporangia abundant near the pinna stalk, sometimes obscuring most of the lower pinna surface, the stalk short, of 2 tiers, sometimes elongate, the lower one with intercalary cell divisions and darker, the annulus of 18-23 indurated cells. Spores tan to light brown, smooth, with a moderately broad, equatorial wing, the 3 angles slightly projecting.

The species is endemic in the state of Mérida but has been collected on three different páramos. The pinnae are exceptionally long and the two lateral lobes at the base are comparable in size and form to the complete, orbicular pinnae in other species. The elongate form of the pinnae, is accompanied by an extended system of veins with a prominent central vein. In these characters and also in the pattern of elongate cells in the upper epidermis, Jamesonia auriculata appears to be closer to species in Eriosorus than to other species in Jamesonia. It occurs at relatively low altitudes for the genus.

Mérida, Venezuela, at 2600-2900 m. Additional specimens examined: VENEZUELA. MERIDA: Páramo del Molino, Jahn 957 (B, BM, GH, US, VEN), 958 (GH, US, VEN); Páramo de Pozo Negro, Steyermark 56291 (GH, K, US).

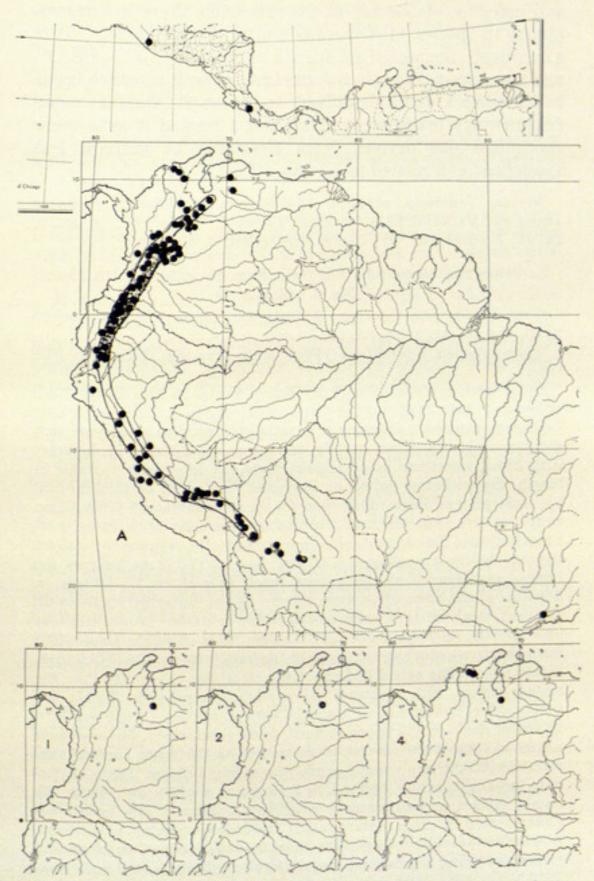
Jamesonia laxa (Mett. ex Kuhn) Diels, in Nat. Pflanz. 1⁴: 260. 1899. Fig. 2. Map 2

Gymnogramma laxa Mett. ex Kuhn, Linnaea 36: 69. 1869. TYPE: Engel 117, Venezuela, Mérida B!, photos: COL, F, GH, NY, US; isotypes B! LE! US!.

Psilogramme laxa (Mett. ex Kuhn) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 333. 1882.

Rhizome not seen. Petiole estimated at 1/10 the length of the lamina, castaneus or atropurpureus, terete, ca. 0.5-1.0 mm. in diameter at the apex, more slender below, glabrous or with sparse, light brown trichomes similar to those of the rachis. Lamina once pinnate, ca. 26-66 cm. long, 0.3-1.0 cm. wide, the apex and base narrowed, with constricted zones of smaller pinnae in the central portion, with ca. 100-350 pinnae, indeterminate, the apical bud smaller than the mature pinnae with trichomes matted or slightly appressed. Rachis castaneus or atropurpureus, usually lighter colored than the petiole, terete or trigonous and the upper surface with an obtuse angle, usually sparsely pubescent, the trichomes not exceeding the length of the pinnae, ruddy brown the basal cells sometimes clear, the apical cell acuminate. Pinnae alternate or subopposite, 2 ranked laterally disposed, distant or approximate, imbricate near the apex, (the basal ones smaller, distant, sterile, finally deciduous, sometimes flat and broadly dentate) rotundate-cordate, plane the margin incurved or scarcely enrolled, inequillateral at the base, 2-5 mm. long, 2-7 mm. wide, bright green, delicate herbaceous; upper surface with sparse to dense tan trichomes, the epidermal cell walls unthickened; lower surface especially the central portion with dense, bright rust-brown, crispate trichomes of few cells, stalk oblique or slightly bent, 0.5 mm. long, the dark color of the stalk extending into the adjacent veins of the pinnae and apparent on both surfaces. Veins slender, in the plane of the upper surface, dichotomous with moderately wide angles, the branches long, the ends clavate to somewhat acute, extending to the margin. Border narrow, one or a few cells broad, irregularly dentate, whitish or lutescent. Sporangia few, mostly adjacent to the pinna stalk, sometimes filling most of the lower surface, the stalk short of 2 or 3 tiers with intercalary cell divisions, the annulus of 15-21 indurated cells. Spores light tan, verrucose, with a broad equatorial wing, the angles prominently projecting; sometimes shriveled.

The species is known from only three collections of leaves, taken about a hundred years ago in the Sierra Nevada de Mérida. The leaves are unusual in having pinnae of a more delicate texture than most of the Andean species of Jamesonia and they are nearly flat with scarcely enrolled margins. In the widely spaced position of the pinnae and their shape



Mars A, 1, 2, 4. Map A, Distribution of Jamesonia, the outline enclosing the least common area of all species, the shaded area is the region of species concentration. Map 1, J. auriculata. Map 2, J. laza. Map 4, J. Cuatrecasasii.

and margins, elaborated at the vein ends, there is a resemblance to species in *Eriosorus* and to *J. rotundifolia*. It is a relatively unspecialized species compared to *J. canescens* and more specialized than *J. auriculata*, both of which occur in the same area. It is difficult to assess the species on the fragmentary material available but I regard it as a more specialized one derived from *Eriosorus* or perhaps less specialized and related to *J. rotundifolia*.

Mérida, Venezuela, at 3050, 4270-4420 m. Additional specimens examined: VENEZUELA. MERIDA: Funck & Schlim 1118 (B, BM, G, LE, P); Karsten (LE, W); Linden 519 (B, BM, G, K, L, P).

Jamesonia rotundifolia Fée, Mém. Fam. Foug. 7: 41, t. 10. 1857.
 Fig. 3. Map 3

TYPE: Schlim 363, Colombia, 8,000-10,000' (3000 m.); isotypes: G! K! P!, photos: COL, F, GH, NY, US.

Gymnogramma rotundifolia (Fée) Mett. Ann. Sci. Nat. V,2: 209. 1864.

Psilogramme rotundifolia (Fée) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 334. 1882.

Rhizome somewhat creeping or especially on smaller plants compact, dichotomously branching, usually slender ca. 0.5-2.5 mm. in diameter with dense, sometimes long, compact roots, the internodes variable in length, the trichomes patent or appressed, castaneus or light brown, the same color or more ruddy than the rhizome surface, 1-3 mm. long, with usually 1 (-4) cells near the base, apex usually acuminate, sometimes bulbous. Petiole bent, often appressed to the rhizome for a short distance before ascending, 1.5-9.0 cm. long, 1/17-1/3 as long as the lamina, castaneus or atropurpureus, terete or oval, ca. 1.5-2.0 mm. in diameter at the apex, often more slender below, moderately pubescent, the trichomes similar to those of the rachis or darker brown. Lamina once pinnate, ca. 14-65 cm. long, 0.7-1.5 cm. wide about the same width throughout or somewhat narrowed at the base, with ca. 100-350 pinnae, indeterminate, the apical bud about the same size or smaller than the mature pinnae, with trichomes not or slightly appressed. Rachis castaneus, often lighter colored than the petiole, terete or trigonous with an obtuse angle on the upper surface, densely pubescent, the trichomes nearly as long as the pinnae, often matted on the lower surface, tan, ruddy or dark brown usually acuminate rarely bulbous. Pinnae alternate, usually laterally disposed in 2 ranks or slightly overlaying the rachis, distant, approximate, or sometimes imbricate, (the basal ones distant, sterile, often deteriorated) rotundate-cordate, patelliform, especially the older pinnae, the margin more or less enrolled and partly obscuring the border, inequilateral at the base, 2-6 mm. long, 1.5-9.0 mm. wide, light green, herbaceous; upper surface more or less pubescent, especially the distal portion with light brown, tan or sometimes gold colored trichomes, with epidermal cell walls unthickened; lower surface more or less pubescent with tan or clear, curled, 1 or few

celled trichomes, or glabrous sometimes with a tuft of trichomes on the stalk or adjacent veins, stalk oblique or bent, ca. 0.5-1.0 mm. long, the dark color often extending into the larger veins of the pinnae especially evident on the lower pinna surface. Veins moderately broad, in the plane of the upper surface or sometimes sunken, dichotomous, the angles moderately wide to acute, the branches long, the ends acute, extending into the border. Border moderately broad, extended at the vein ends, irregularly dentate, whitish, clear or lutescent, sometimes little modified and similar to the texture of the pinna. Sporangia abundant adjacent to the pinna stalk sometimes crowded and obscuring the lower surface, the stalk usually short of 2 tiers each of 3 cells which are sometimes elongated and the lower darker, the annulus of 17-19 indurated cells. Spores light tan, verrucose, especially on the distal face, nearly smooth on the proximal face with a broad, sometimes lobed equatorial wing, the 3 angles not or slightly projecting.

Morphologically, Jamesonia rotundifolia is intermediate to a few less specialized species and to several which are more specialized. Compared to the less specialized ones, which are local in occurrence, it is geographically wide ranging from central Peru to Costa Rica. The characters are also generalized, rather than unique and on the basis of this and on the broad distribution, J. rotundifolia is regarded as a possible source from which one or more of the derived

species might have originated.

On the ten páramos on which I collected in Colombia, Jamesonia rotundifolia occurred in abundance on six and where it occurred with J. imbricata var. glutinosa there were specimens intermediate between these two. Two collections, from Páramo de las Puentas, above La Baja, Santander, Colombia, Killip & Smith 18191 and 18208, are difficult to place. I am referring them to this species on similarities in the rhizome trichomes, the pinna form and orientation of the pinnae stalks although the specimens have exceptionally broad, membranous borders and dense tomentum on the lower surface of the pinnae for this species. Jamesonia imbricata var. glutinosa, J. bogotensis and J. robusta also occur in the region and it is possible that these specimens may be intermediate between J. rotundifolia and one of these, especially the last.

Costa Rica to Central Peru, at 2600-4200 m. Additional specimens examined: COSTA RICA. H. Carson in 1956 (GH). CARTAGO: Cerro de la Muerte, Holm & Iltis 529 (B, BM, S-PA, US); Cerro du Buena Vista, Pittier & Tonduz 3348 (P, US); Cerro de la Muerte, Scamman 6079 (GH); Scamman & Holdridge 7928 (GH). SAN JOSE: Cerro de las Vueltas, Pittier 10504 (BM, GH, K, LE, P, US); Cerro de las Vueltas,

Standley & Valerio 43847 (GH, US). COLOMBIA. CAUCA: Páramo de Guancas, Lehmann 5706 (B, F, K, P, US); von Sneidern 2176 (GH, S); Tryon & Tryon 5992 (GH), Páramo de Puracé, 5959 (BM, COL, GH, LE, US); Yepes-Agredo 544 (COL). CUNDINAMARCA: Páramo de Guasca, Alston 7455 (BM, GH, US), 7459 (BM, GH, US); André 1534 (K); Páramo de Chipaque, Apolinar-Maria 23 (US); Bischler 1261 (COL); Guadalupe, Cuatrecasas 5579 (US), Páramo de Guasca, 9494 (COL, US); Páramo de Guasca, Fosberg & Valencia 21449 (GH, US); La Herrera, Garcia-Barriga 10911 (COL), Páramo de Guasca, 11660 (COL, US); Alto de la Cruces, Grant 9555 (US); Guadalupe, Haught 5652 (COL, S-PA, US), 5653 (COL, US); Holton in 1854 (COL, G, GH); Páramo de Guasca, Killip 34095 (COL, GH, K, US); Lindig 83, from San Fortunato (BM), from Choachi (B, K, P), from Fusagasuga (K); Little & Little 7433 (COL, US), 7436 (COL, US); El Peñon, Pennell 2657 (GH, US); Páramo de Guasca, Tryon & Tryon 5915 (BM, COL, GH, LE, NY, P, US, VEN), Páramo de Palacio, 6040 (BM, GH, US), 6053 (GH), Alto de Aguila, 6071 (BM, GH), 6072 (BM, COL, GH), Páramo de Cruz Verde, 6081 (GH). NORTE DE SANTANDER: La Mesita, Alston 7232 (BM, GH); Páramo de Romeral, Killip & Smith 18658 (COL, GH, US), Páramo de Santurbán 19592 (GH, US); Páramo Almorzador, Vareschi 4044 (VEN). SANTANDER: Kalbreyer 726 (US); Páramo de las Vegas, Killip & Smith 15695 (GH, US), Páramo Rico, 17752, 17812 (GH, US), Páramo de las Puentes, 18191 (COL, GH, NY, US), 18203 (COL, GH, US), Páramo de Vetas, 21180 (GH, US). VALLE: Páramo de Bavaya, Cuatrecasas 20223 (GH, US). ECUADOR. TUNGURAHUA: Asplund 9882 (GH, S). PERU. HUANUCO: Bryan 612 (F). PIURA: Weberbauer 6076 (B, F, GH, US).

4. Jamesonia Cuatrecasasii A. F. Tryon, sp. nov. Fig. 4. Map 4

Trichomata rhizomatis rigida, appressa, obscuro-fusca vel atropurpurea, rachis tomento fulvo vel rufo-fusco, pinnae valde imbricatae et appressae, ovato-rotundatae, patelliformes herbaceae, 3.0-4.5 mm. longae, 3-5 mm latae, petioluli breves adaxialiter supra pinnas, pinna adaxialiter pubescens, abaxialiter glandulis capitatis vel trichomatibus sparsis, nervis latis, dichotomis, angulis latis, limbo angusto vel modice lato, dentato, sporae fulvae vel pallido-fuscae, papillatae.

TYPUS: Colombia, Dept. Magdalena, Sierra Nevada de Santa Marta, rocky and meadowy páramos around Laguna Naboba, Laguna Mamito and Laguna Mamo, 4200-4300 m. Oct. 3, 4, 5, 1959, J. Cuatrecasas and R. Romero Castaneda 24613, US.

Rhizome creeping, ca. 3-4 mm. in diameter with few, coarse roots, the internodes short (in one specimen), the trichomes rigid, appressed, lustrous dark brown or atropurpureus, darker than the rhizome surface, 1.0-1.25 mm. long, with 3-6 cells near the base, apex acuminate. Petiole bent near the rhizome, 4.0-8.5 cm. long about 1/9 or 1/4 as long as the lamina, castaneus, terete, ca. 1-2 mm. in diameter at the apex, slightly more slender near the rhizome, more or less tomentose, the trichomes similar to those of the rachis but shorter and not as broad. Lamina once pinnate, 26, 35, 38 cm. long, 0.6-1.4 cm. wide, the lamina broadest at the apex narrowed toward the base with ca. 350-500 pinnae, indeterminate, the apical bud larger than the mature

pinnae, with trichomes patent or slightly appressed. Rachis castaneus or tan, terete or ellipsoidal, tomentose, the trichomes exceeding the length of the pinnae 1 or 2 times, usually matted, tan or rust brown, with the basal cells usually clear, the apical cell acuminate or short bulbous. Pinnae subopposite, appressed in 2 ranks, and strongly imbricate, (the basal ones minute, distant, sterile) ovate-rotundate, the acroscopic lobe sometimes slightly elongate, patelliform, the margins enrolled, wholly or partly obscuring the border, inequilateral at the base, 3.0-4.5 mm. long, 3-5 mm. wide, light green, herbaceous; upper surface pubescent with tan, gold, or rust colored trichomes especially abundant on the distal part and also with shorter trichomes similar to those of the lower surface, with epidermal cell walls unthickened; lower surface with 2 or 3 celled capitate glands, sometimes also with sparse trichomes similar to but shorter than those of the upper surface, stalk straight, ca. 0.5 mm. long, castaneus, attached to the upper surface of the pinna, often articulating in the mid-portion. Veins broad, slightly sunken, dichotomous with wide angles, branches short to moderately long, the ends acute or clavate, extending to the border. Border narrow to moderately broad, membranous more or less dentate with sparse trichomes, tan. Sporangia sparsely distributed along the veins, the stalk short, of 2 tiers, sometimes elongate, the lower tier usually darker, the annulus of 19-21 indurated cells. Spores tan to medium brown, papillose, with a moderately broad equatorial wing, the 3 angles slightly projecting.

I am pleased to name this unique species from the Sierra Nevada de Santa Marta for Dr. José Cuatrecasas. His numerous collections of *Jamesonia* from Colombia and the completeness of his specimens have enabled me to know the species of *Jamesonia* and their distributions more fully.

The species is unusual in the genus in having the pinna stalks affixed to the upper surface of the pinnae. This condition appears to be an extreme expression of a trend toward the simplification of the lamina. The position of the pinna stalk in Jamesonia Cuatrecasasii actually appears to be the result of a combination of modified characters. The stalk has been shortened and the tissue at the base of the pinna adjacent to the stalk has coalesced about the lower surface of the stalk. In addition to these changes there has been a realignment of the pinnae in a closely compressed and imbricate or incubous arrangement especially in the apical portion of the leaves.

There is a record of this species from the Sierra Nevada de Mérida from the Jahn collection which is a mixture of this and *Jamesonia canescens*. There is a resemblance between these two species in the copious tomentum of the leaves but in *J. Cuatrecasasii* much of the indument which envelops the lower surface of the leaf is attached to the distal portion of the pinnae while in *J. canescens* it is largely the rachis tomentum which envelops the pinnae. In the patelliform and rotundate form of the pinnae and the light colored tomentum which envelops them there seems to be a greater resemblance between *J. rotundifolia* and *J. Cuatrecasasii* than between the latter and *J. canescens*.

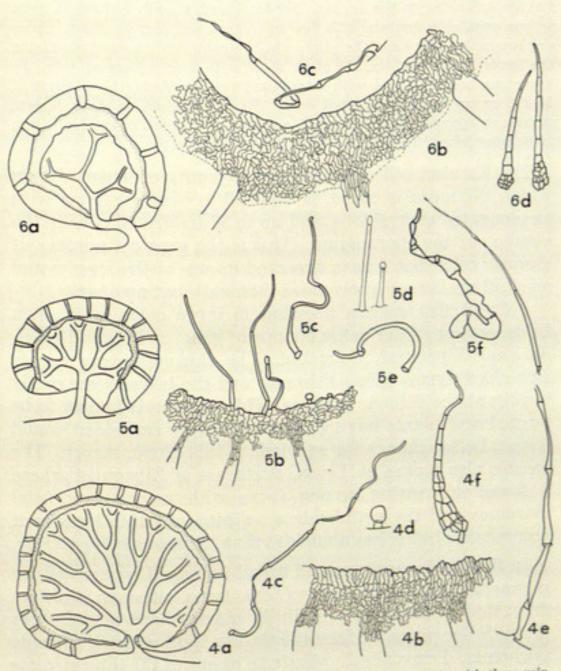
Colombia and Venezuela at 3500-4400 m. Additional specimens examined: COLOMBIA. MAGDALENA: Barclay & Juajibioy 6560 (GH), Páramo de Macotama, 6933 (GH); Cabot 27 (GH); Schlim 850 (B, BM, G, K, L); Seifriz 500 (US); Wolleston 15 (K). VENEZUELA. MERIDA: Jahn 137 (G, US).

Jamesonia robusta Karst. Fl. Columb. 2: 29, t. 115. 1862. Fig. 5. Map 5

TYPE: H. Karsten, Colombia, Bogotá, LE!, photo GH; isotype: W!, photo BM!, GH.

Gymnogramma robusta (Karst.) Hieron, Engl. Bot. Jahrb. 34: 476. 1904.

Rhizome long creeping, dichotomously branching, often slender, ca. 0.5-2.0 mm. in diameter with many short, delicate roots, the internodes variable in length, the trichomes sparse, lax, patent, tan or light brown, lighter or the same color as the rhizome surface, 0.5-1.5 mm. long, usually with 1 cell, rarely 2 near the base, apex with a bulbous cell or acuminate. Petiole usually bent and appressed to the rhizome for a short distance before ascending, 4-10 cm. long, 1/5 to 1/3 as long as the lamina, castaneus to atropurpureus, terete or ellipsoidal, ca. 0.5 mm. in diameter at the apex usually more slender near the rhizome, with sparse, tan trichomes similar but shorter than those of the rachis. Lamina once pinnate, 24-36 cm. long, 0.3-0.7 cm. wide about the same width throughout or slightly broader at the apex with ca. 130-330 pinnae, indeterminate, the apical bud larger than the mature pinnae, with patent trichomes. Rachis castaneus or atropurpureus, terete or trigonous with an obtuse angle on the upper surface, pubescent, the trichomes equal to or usually up to two times longer than the pinnae, usually more densely tomentose on the lower surface, rust brown with the cells near the apex often grayed especially on older leaves, the apical cell acuminate. Pinnae alternate, subopposite in the apical portion of the lamina, 2 ranked, laterally disposed or slightly overlaying the rachis, imbricate, (basal pinnae smaller, distant, sterile, finally deciduous or often persistent) reniform, rarely with a slightly elongate central lobe, plane, margin enrolled, inequilateral at the base, 2-4 mm. long, 3-5 mm. wide, bright green, herbaceous; upper surface glabrous or slightly pubescent in the distal portion the trichomes tan or rust colored, with epidermal cell walls unthickened; lower surface with sparse to moderately dense rust brown, curled trichomes and shorter, capitate, glandular trichomes, stalk straight, ca. 0.5-1.0 mm. long, tan or light brown, not articulate. Veins broad, especially near the pinna



Figs 4-6. Fig. 4. J. Cuatrecasasii: a, pinna, × 10; b, pinna margin with three vein ends, × 35; c, trichome from upper pinna surface, × 30; d, gland from lower pinna surface, enlarged; e, rachis trichome with four cells omitted from the mid-portion, × 30; f, rhizome trichome, × 30; all from Cuatrecasas & Castaneda 24613 (US). × 30; f, rhizome trichome, × 30; d, capitate trichomes from lower pinna trichome from upper pinna surface, × 30; d, capitate trichomes from lower pinna surface, × 30; the last five from Aspsurface, × 30; e, trichome from lower pinna surface, × 30; the last five from Aspsurface, × 30; from Hitchcock 21638 (GH). Fig. 6. J. lund 17827 (GH); f, rhizome trichome, × 30, from Hitchcock 21638 (GH). Fig. 6. J. pulchra: a, pinna, × 10, from Ewan 16100 (GH); b, pinna margin with three vein ends, the broken line indicating the limit of the border, × 35, from Pennell & Hazen 10068 (GH); c, rachis trichome, × 30, from Cuatrecasas 20124 (GH); d, rhizome trichomes, × 30, from Pennell & Hazen 10068 (GH).

stalk, in the plane of the upper surface or slightly raised, dichotomous with wide angles, the branches moderately long, the ends acute or clavate extending to the border. Border broad, usually indusioid, more or less regularly dentate with few trichomes and glands, clear. Sporangia usually few near the pinna stalk, sometimes crowded obscuring the lower pinna surface, the stalk short with 2 or 3 tiers of cells, the lower one brownish and with intercalary cell divisions, the annulus of 24-27, or up to 33 indurated cells. Spores medium to dark brown, smooth or sparsely papillose, with a moderately broad equatorial wing, sometimes lobed, the angles not or slightly projecting.

The Karsten collection from the vicinity of Bogotá, upon which the name is based, is atypical in having pinnae with an elongated central lobe, and up to 33 indurated cells in the annulus of the sporangium. This is the greatest number of annular cells that I have observed in any of the species and most others have slightly more than half that number.

I found this species growing in large colonies in open fields, among rather dense clumps of grass at Patano Redondo, near Zipaquirá, Colombia. The rhizomes were deeply embedded among grass rhizomes and the leaves were easily broken at the delicate petioles. This páramo is known to be burned and plants having portions deeply embedded would have a better chance for survival in this circumstance. The species also occurs at Tausa, northeast of Zipaquirá where I found it growing among rocks with rather superficial rhizomes and the petioles less delicate. At this locality it occurs with, but is less abundant than, Jamesonia bogotensis.

In the reniform shape and broad indusioid borders of the pinnae, *J. robusta* resembles *J. canescens*, although it differs from that species in the relatively sparse, discrete trichomes on the lower pinna surface and the lax, light colored, rhizome trichomes. I consider *J. robusta* to be one of the intermediate species, more specialized than *J. rotundifolia* and less specialized than *J. canescens*.

Northern Colombia to southern Ecuador, at 2700-3570 m. Additional specimens examined: COLOMBIA. Apollinaire-Maria 16 (US); Ariste-Joseph A213 (US). BOYACA: Páramo de Rusia, Langenheim 3442 (US). CUNDINAMARCA: Páramo de Choachi, Apollinaire 12 (US); Little & Little 9450 (COL, US); Mt. Aquila, Pennell 2530 (GH, K, US); Patano Redondo, Tryon & Tryon 6055 (BM, COL, GH, NY, P, US), Tausa, 6157A (B, COL, GH, US). ECUADOR. AZUAY: Asplund 17827 (GH, S); Páramos de Silván, Barclay & Juajibioy 8372 (GH); Hitchcock 21638 (GH, US); Jameson (K, US); Páramo Tinajillas, Wiggins 10784 (US). CANAR: Prieto P-143 (GH). PICHINCHA: Jameson (F, G, K).

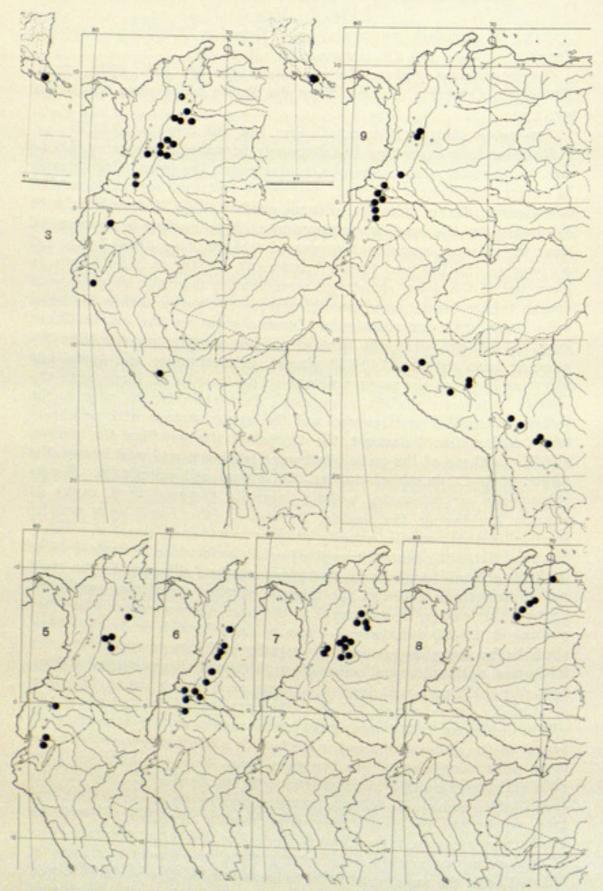
Jamesonia pulchra Hook. and Grev. Icon. Fil. 2, t. 178. 1830.
 Fig. 6. Map 6

TYPE: W. Jameson, monte Cayambe, Ecuador, 12,000 ped., (cited as Peru) E!, photos: BM, GH, isotype: Herb Hook. K!.

Gymnogramma glabra Hieron. Hedwigia 48: 215. 1909. TYPE: Stübel 69, Colombia, Tolima, Boca del Monte B!, photos: COL, F, GH, NY, US.

Jamesonia glabra (Hieron.) C. Chr. Ind. Fil. Suppl. 47. 1913.

Rhizome long creeping, dichotomously branched, slender ca. 1.0-2.5 mm. in diameter with numerous, coarse roots, the internodes variable in length, the trichomes rigid, appressed, lustrous, atropurpureus or dark brown, darker than the rhizome surface, 0.5-1.25 mm. long, with 1-4 cells near the base, apex acuminate. Petiole often bent or curled near the rhizome, sometimes appressed 4-16 cm. long, about 1/8 or 1/5 as long as the lamina, shining, castaneus, terete, ca. 0.5-1.0 mm. in diameter at the apex, sometimes more slender near the rhizome, with sparse tan or brown sometimes bicolorous trichomes having the basal cells clear, the apex acuminate. Lamina once pinnate, ca. 19-45 cm. long, 0.3-0.8 cm. wide, the central portion usually broader than the apex or base with ca. 140-350 pinnae, indeterminate, the apical bud about as large as the mature pinnae or up to twice as large, with trichomes patent or slightly appressed. Rachis similar in color to the petiole, ellipsoidal or trigonous and the upper surface with an obtuse angle and sparse indument, the trichomes shorter than the pinnae, similar to those of the petiole but usually longer and rust brown, the upper portion sometimes darker, the apical cell acuminate. Pinnae subopposite or alternate, usually laterally disposed in 2 ranks or slightly overlaying the rachis, imbricate, (the basal ones usually smaller, distant, sterile, usually gray or weathered, sometimes membranous, flat, with dentate margins) orbicular-cordate or ovate-cordate with an oblique base, plane, the upper surface adjacent to the stalk not or sometimes concave, the margin enrolled sometimes partly obscuring the border, inequilateral at the base, the acroscopic lobe often prolonged, 1.5-4.0 mm. long, 1-4 mm. wide, yellowish or bright green, rigid herbaceous; upper surface usually glabrous or with few, tan trichomes, with epidermal cell walls unthickened; lower surface tomentose, the trichomes rust brown, crispate of 1 or few cells, stalk bent or strongly curved nearly 90° and often overlaying the acroscopic lobe of the pinna, ca. 1.0-1.5 mm. long, tan to castaneus. Veins moderately broad, in the plane of the upper surface or sometimes sunken, dichotomous with wide angles, the branches short or moderately long, the ends clavate extending to or shortly into the border. Border usually broad, often indusioid, delicate membranous, entire or somewhat dentate, ruddy tan or clear. Sporangia usually abundant, protruding above the tomentum, throughout the length of the veins, the stalk short of 3 tiers or moderately long with 4 tiers, the lowest a cluster of inflated cells, the annulus of 16-24 indurated cells. Spores light brown, smooth or with few broad ridges on the distal face, the equatorial wing moderately broad, the 3 angles not or slightly projecting; often shriveled.



Mars 3, 5-9. Map 3, J. rotundifolia. Map 5, J. robusta. Map 6, J. pulchra. Map 7, J. bogotensis. Map 8, J. canescens. Map 9, J. Scammanae.

After Hooker and Greville described this species they retracted it in the addenda of their work with the following comment, "Tab. 178 Jamesonia pulchra. We are assured by Kaulfuss that this Fern is the Pteris imbricata of Swartz. The descriptions given of it, however we find to be incorrect. For Jamesonia pulchra, therefore, read J. imbricata". The Jameson collection upon which this name is based, in the Greville Herbarium at Edinburgh is mounted with a collection from Peru, Mathews 979. The Jameson collection from Cayambe, consists of two leaves, each representing a different species and neither of them J. imbricata. The larger leaf is from a plant of this species and the other is one from J. robusta. Both the description and figures of this material in the Icones Filicum are so generalized that it is not possible to positively identify either species as the predominant element of the treatment. The illustration of the straight pinna stalks applies better to J. robusta, but on the gross aspect of the larger apical bud, the more distantly spaced pinnae and the bent petioles there is a greater resemblance between the illustration and the larger leaf of the original collection. I am applying the name J. pulchra to this and the smaller leaf is now identified as J. robusta.

The strongly bent pinna stalks and prolonged basal lobe of the pinna in *J. pulchra* are rather distinctive, specialized characters. The tomentum on the lower surface of the pinnae and the broad indusioid borders show a similarity to *J. robusta* and the rigid, appressed rhizome trichomes are similar to those in *J. canescens*. It appears to be one of the species intermediate to these and with relatively specialized characters.

Cordillera Central of Colombia to northern Ecuador, at 3000-4270 m. Additional specimens examined: COLOMBIA. ANTIQUIA: Páramo de Chaquiro, Pennell 4270 (GH, US), 4282 (GH, K, US). CALDAS: Cuatrecasas 23105 (GH, US); Páramo del Quindio, Pennell & Hazen 9939 (GH, US), 10068 (GH, US); Páramo Ruiz, Tryon & Tryon 6141 (COL, GH). CAUCA: Cuatrecasas 18966 (GH, US), 19112 (GH, US); Páramo de Gabriel Lopéz, Lehmann V. in 1961 (GH); Páramo de Buena Vista, Pittier 1136 (US); Páramo de Puracé, Tryon & Tryon 5972 (B, BM, COL, GH, LE, NY, US). NARINO: Volcán de Chiles, Ewan 16100 (GH, US), Volcán de El Galeras, Ewan 16315 (GH, US). PUTUMAYO: Páramo de Bavaya, Cuatrecasas 20124 (G, GH, US); Alta de Cruz, Foster & Foster 2052 (COL); Páramo de San Antonio, Schultes 3239 (GH, US). TOLIMA: Páramo Ruiz, Pennell 3089 (GH, K, US). ECUADOR. CARCHI: Holmgren 881 (B, BM, F, G, GH, K, S-PA, US).

7. Jamesonia bogotensis Karst. Fl. Columb. 2: 29, t. 115. 1862. Fig. 7. Map 7

TYPE: H. Karsten, Colombia, Tausa LE! photo, GH, W; isotypes: LE!, W! photo BM!.

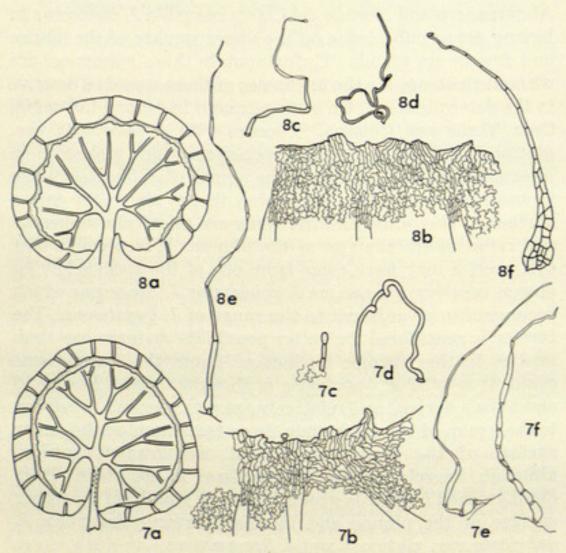
Gymnogramma bogotensis (Karst.) Hieron. Engl. Bot. Jahrb. 34: 478. 1904.

Rhizome long creeping, dichotomously branching, ca. 1-4 mm. in diameter with numerous, coarse roots, the internodes variable in length, the trichomes lax, patent, lustrous, light amber color or light brown, usually lighter than or the same color as the rhizome surface, 1-2 mm. long with 1 cell at the base, apex acuminate. Petiole usually bent or curled and sometimes appressed to the rhizome for a short distance before ascending, 1-7 cm. long, 1/10-1/4 as long as the lamina, atropurpureus, terete or ellipsoidal, ca. 1.0-2.5 mm, in diameter at the apex, more slender near the rhizome with sparse tan trichomes similar to but often shorter than those of the rachis. Lamina once pinnate, ca. 10-35 cm. long, 0.3-0.6 cm. wide about the same size throughout or somewhat narrowed toward the base, with ca. 120-570 pinnae, indeterminate, the apical bud usually larger than the mature pinnae, with patent trichomes. Rachis castaneus, terete or trigonous with an obtuse angle on the upper surface, the upper surface pubescent, the lower surface tomentose, the trichomes equal to or slightly longer than the pinnae, not enveloping them except near the lamina apex, concolorous, tan or ruddy brown becoming gray above, the apical cell acuminate, rarely bulbous on the bud. Pinnae subopposite, laterally disposed, usually stacked in 2 ranks, imbricate, (the basal ones smaller, distant, sterile, persistent) ovate-cordate or orbicular-cordate, the basal lobes usually prolonged and protruding above the upper surface of the pinna, usually concave on the upper surface adjacent to the stalk, the margin enrolled partly or wholly obscuring the border, inequilateral at the base, 2-4 mm. long, 2-4 mm. wide medium or bright green, herbaceous; upper surface glandular, usually glutinose or crustose, also sometimes pubescent, the trichomes tan or clear, the epidermal cells unthickened; lower surface densely tomentose and matted, the trichomes crispate, 1 or few celled, also with short, capitate glands especially near the border, stalk straight, ca. 0.5-1.0 mm. long, tan or castaneus sometimes glandular, often articulating in the mid-portion. Veins broad, usually sunken especially the main veins near the stalk, sometimes slightly raised, dichotomous with wide angles, the branches short or moderately long, the ends clavate or acute, extending to the border. Border usually moderately broad, rarely broader, more or less regularly dentate, sometimes glandular, tan or rust brown. Sporangia usually abundant and enmeshed in the tomentum throughout the length of the veins, the stalk short, up to half as long as the capsule, with 2 or 3 tiers of cells these sometimes elongate, the annulus with 19-25 indurated cells. Spores tan to light brown, verrucose or irregularly papillose, with a moderately broad equatorial wing sometimes irregular, the angles not projecting.

Most specimens of this species are relatively easily identified but a few from northeastern Colombia on Páramo

Almorzadero and Nevado del Cocuy resemble J. canescens in having dense pubescence on the upper surface of the pinnae and few or no glands. Unfortunately these specimens are without rhizomes for the trichomes of these would be decisive in the determination. On some páramos in central Colombia, Cruz Verde and Chisaca, it occurs with J. imbricata var. glutinosa and there are some specimens which appear to be intermediate between them. The pinnae of J. bogotensis are unusual in having the basal lobes thrust above the upper surface of the pinna and the veins are relatively numerous and crowded for the size of the pinnae. It is possible that this species may have come from one of the species having larger, reniform pinnae, as J. robusta or J. canescens which occur within or adjacent to the range of J. bogotensis. The former is considered the better possibility as there are similarities in the rhizome trichomes. From the chromosome count of n = 87 J. bogotensis is thought to be a hexaploid and to be a derived and relatively complex species. It belongs to the group of species having dense tomentum on the under surface of the pinnae and broad, membranous borders although its relationship among these is not clear. It is distinguished from this group in having glands on the upper surface of the pinnae and in this character resembles J. imbricata var. glutinosa and J. Scammanae.

Central Colombia northeast to the Venezuelan border, at 2950-4400 m. Additional specimens examined: COLOMBIA. Páramo de Cachene, Austin 25 (K); Wercklé in 1906 (GH). BOYACA: Barclay & Juajibioy 7396 (GH); Chorreón de San Paulino, Cuatrecasas & Garcia-Barriga 1328 (COL, US), 1421 (US). CALDAS: Cuatrecasas 23225 (GH, US); Páramo del Quindio, Pennell & Hazen 9931 (GH, US). CUNDINAMARCA: Apollinaire, in May 1905 (GH, P), in April 1906 (GH); Páramo de Zipaquirá, Cuatrecasas 9540 (COL, US); Fosberg 22022 (GH, US); Goudot (G); Lindig 185 (K); Little 9313 (US); Mutis 3097 (US); Pérez Arbeláez 1153 (COL, US), 1490 (US); Páramo de Chisaca, Schultes 20172 (COL, GH, US); Páramo de Cruz Verde, Tryon & Tryon 6080 (BM, COL, GH, P, US), Tausa, 6156 (GH), 6157 (B, COL, GH, LE, NY, P, US), Páramo de Chisacá, 6177 (B, BM, COL, F, GH, LE, NY, P, US), 6178 (GH). NORTE DE SANTANDER: Funck & Schlim 1370 (BM, G, L, LE, P). SANTANDER: Páramo de Almorzaderos, Alston 7386 (BM, GH); Apolinar-Maria 20 (US); Cuatrecasas 10032 (US), 13514 (COL, GH, US); Páramo de las Vegas, Killip & Smith 15658 (COL, GH, S, US), Páramo de Vetas, 17412 (BM, COL, GH, US), Páramo de Santurbán, 17575 (B, GH, P, US), Páramo de Mogotocoro, 17647 (GH, US), Páramo Rico, 17725 (GH, US), Páramo de las Coloradas, 18446 (GH, K, LE, S-PA, US); Almorzador, Vareschi 4040 (VEN), 4041 (VEN).



Figs. 7 and 8. Fig. 7. J. bogotensis: a, pinna, × 10; b, pinna margin with three vein ends, × 35; both from Schultes 20172 (gH); c, glandular trichome from upper pinna surface with epidermal cells, enlarged, from Cuatrecasas 13514 (gH); d, trichome from lower pinna surface, × 40, from Killip & Smith 18446 (gH); e, rachis trichome, × 30, from Cuatrecasas 13514 (gH); f, rhizome trichome, × 30, from Killip & Smith 17647 (gH). Fig. 8. J. canescens: a, pinna, × 10; b, pinna margin with three vein ends, × 35; c, trichome from upper pinna surface, × 45; d, trichome from lower pinna surface, × 30; the last four from Gabaldon, in 1922 (US); e, rachis trichome, × 30, from Alston 6601 (gH); f, rhizome trichome, × 30, from Alston 6815 (gH).

Jamesonia canescens Kunze, Farrnkr. 1: 95. 1846. Fig. 8 Map 8

TYPE: Moritz 339, Venezuela, Páramo de la Culata (cited as Colombia by Kunze) B!, photos COL, F, GH, NY, US; isotypes: BM! E! G! GH! K! P! US!.

Gymnogramma canescens (Kunze) Kl. Linnaea 20: 407. 1847.

Jamesonia nivea Karst. Fl. Columb. 2: 29, t. 115. 1862. TYPE: H. Karsten, Venezuela, Prov. Mérida, Jaji, LE! photos, GH, W; isotypes: LE! P! W!; photos BM, GH.

Jamesonia imbricata (Sw.) Hook. and Grev. var. canescens (Kunze)

Hook. Sp. Fil. 5: 106. 1864.

Psilogramme canescens (Kunze) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 333. 1882.

Psilogramme nivea (Karst.) Kuhn. op. cit. 333. 1882.

Jamesonia imbricata (Sw.) Hook. and Grev. var. nivea (Karst.)

Sodiro, Crypt. Vasc. Quit. 387. 1893.

Rhizome long creeping, dichotomously branching ca. 1-3 mm. in diameter with sparse to numerous coarse roots, the internodes variable in length, the trichomes rigid, appressed, lustrous dark brown to black, darker than the rhizome surface, ca. 1.0-2.5 mm. long with 1-5 cells usually more than 1 near the base, apex acuminate. Petiole usually bent or curled and appressed to the rhizome for a short distance before ascending, 1.5-11.0 cm. long, 1/20-1/3 as long as the lamina, castaneus, terete or ellipsoidal, ca. 1.0-2.5 mm. in diameter at the apex, more slender near the rhizome, with sparse to moderately dense, tan or rust brown trichomes similar to those of the rachis. Lamina once pinnate, ca. 10-50 cm. long, 0.3-1.2 cm. wide, with the apical portion of the lamina broadest, narrowed toward the base, ca. 120-600 pinnae, indete minate, the apical bud larger than the mature pinnae, with patent trichomes. Rachis castaneus, terete or trigonous with an obtuse angle on the upper surface, densely tomentose, the trichomes usually two or more times longer than the pinnae and usually enveloping them, rustbrown, tan or gray, concolorous, the apical cell long acuminate. Pinnae subopposite, laterally disposed, often stacked in 2 ranks, imbricate, (the basal ones smaller, distant, sterile, persistent, sometimes alternate, membranous, flat, with dentate margins) mostly reniform or orbicular, plane or sometimes with the acroscopic lobe prolonged and bent, the margins enrolled, sometimes partly obscuring the border, inequilateral at the base 2-4 mm. long, 1-5 mm. wide, medium green, rigid herbaceous; upper surface usually tomentose, the trichomes usually clear, tan or sometimes darker, the epidermal cell walls unthickened; lower surface with dense tan or rust colored, matted tomentum, the trichomes crispate, 1 or few celled, sometimes also with capitate glands, seldom glabrous, stalk straight (usually bent in intermediate specimens) ca. 0.5-1.0 mm. long, tan to castaneus, sometimes articulate in the mid-portion. Veins broad, especially the main ones adjacent to the stalk, sunken on the upper surface, dichotomously branching at wide angles, the branches moderately long, the ends acute or clavate, extending to the border. Border usually broad, sometimes indusioid, rather regularly dentate, clear or tan. Sporangia moderately dense, enmeshed in the tomentum, the stalk short, up to 1/2 as long as the capsule, with 2 or 3 tiers, the lower usually darker and with intercalary divisions, the annulus with 18-20 indurated cells. Spores tan to light brown, verrucose or irregularly papillose especially on the distal face, with a moderately broad equatorial wing, sometimes irregularly lobed, the angles not projecting.

There is some confusion as to the country of the type collection of Moritz for the description and most of the authentic specimens indicate Colombia. The specimen at the British Museum, appears to have the original ticket and has the following data, "Páramo de la Culata, Chalapa i via Mérida". Both Páramo de la Culata and Mérida are in

Venezuela and evidently an error was made, in copying the label, which was taken up by Kunze. There is also some doubt about which of the specimens represents the type for Kunze cites two specimens, one at Berlin and a second in the herbarium of Moritz which was later acquired by the British Museum. Neither of these specimens bears his annotation nor can they be positively identified with the figure in tab. 133 of his Farrnkräuter Supplement of 1851. I have cited the specimen at Berlin, which is more complete, as the type.

There are a few variations, particularly in the tomentum and size of the leaves of *J. canescens*, which do not merit taxonomic recognition, but should receive some attention. Field studies have been most helpful in the interpretation of some of these. In the Sierra de Santo Domingo around Laguna Negra there are plants on which the lower pinnae of the leaves, or all of them on small leaves, are nearly glabrous, flat and dentate. This appears to be a juvenile form which is retained for a longer period in some plants.

The color of the tomentum of the leaves in Jamesonia canescens varies from white to rust brown with most of the collections in the range between tan and rust colored. Those with grayish white tomentum have been recognized earlier as J. nivea. I have observed plants of this type at several stations in the Sierra Nevada de Mérida and find them to occur in the same habitat as those with darker tomentose leaves but in colonies discrete from them. They have generally more slender leaves and the pinnae are sometimes glabrous on the lower surface. I have included them in J. canescens since I do not find other morphological differences equivalent to those of other species.

The most heavily tomentose plants occurred in large colonies on Páramo de la Negra in Táchira. The leaves were covered with a felted, white tomentum and formed a dense carpet-like growth on the highest part of the páramo. These are quite distinctive plants and can be readily recognized as from this area.

There are several collections with green, sparsely tomentose leaves having small pinnae and usually bent pinnae stalks which occur within the range of Jamesonia canescens, particularly in the northern part of Mérida from páramos Timotes, Gavilan, Pico Aguila, Laguna Negra and Laguna Grande and on páramos Conejos and Quinora near the city

of Mérida. These plants have some resemblance to *J. imbricata* var. *glutinosa* in having elongate pinnae with bent stalks which may be inserted at the pinnae base without a notch, the indument on the upper pinna surface is usually of coarse, short trichomes and on the lower surface it is usually of white or tan, crispate trichomes. There is also a similarity in these characters to *J. imbricata* var. *meridensis* although none of this material is glandular on the upper pinna surface as in that variety. The collections of this variation are cited apart from the others.

Except for collections on Páramo de Táma on the Colombian border all of the specimens are from Venezuela mostly from the Sierra Nevada de Mérida but extending northeast to Lara. It usually occurs above 3500 m. and up to 4400 but has been collected at 2600 m. on Páramo de Molino above Mérida. Additional specimens examined: VENEZUELA. LARA: Steyermark 55493 (GH, K, US). MERIDA: Páramo de Timotes, Alston 6594 (BM, GH), 6601 (BM, GH), Páramo de Mucuchies, 6638 (BM, GH), 6653 (BM, GH), 6815 (BM, GH), 6927 (BM, GH), Páramo de la Negra, 7000 (BM, GH), 7025 (BM, GH); Páramo de Mucubaji, Barclay & Juajibioy 9557 (GH), 9636 (GH), Pico de Mucunuqui 9901 (GH); Bellard 203 (US), 208 (US); Boursey, in Mar. 1901 (GH); Chardon 305 (VEN); Fortanier, herb. no. 19938 (VEN); Funck & Schlim 1097 (B, BM, E, G, L, LE, P); Ewan 16966 (K, US, VEN); Gabaldon, in 1922 (US); Gehriger 79 (G, VEN); Gines 1728 (US); Páramo de Mucuchies, Gutzwiller 13 (VEN), 26 (G); Páramo del Tambor, Hanbury-Tracy 44 (K); Páramo de Timotes, Jahn 138 (G, US), Páramo Quinora 726 (B, US, VEN), 855 (GH, US, VEN), Páramo del Molino, 956 (GH, P, US, VEN), Páramo de San José, 972 (GH, US, VEN), Páramo de Sto. Domingo 1103 (BM, US, VEN), 1308 (VEN); Páramo de Timotes, Pittier 12724 (G, US, VEN); Reed 74 (US); Steyermark 55901 (GH, U, US, VEN); Páramo de El Gavilán, Tamayo 38 (US, VEN), 39 (US, VEN), 40 (US, VEN), 41 (US, VEN), 42 (US, VEN), Páramo de Mucuchies 3803 (VEN), 3804 (VEN); Tryon & Tryon 5796 (BM, GH, US), 5798 (GH), 5800 (BM, COL, GH, NY, US), 5800 (GH), 5809 (B, GH, LE, P), 5812 (GH), 5819 (GH), 5824 (GH, NY), 5826 (GH, US), 5827 (F, GH), 5828 (GH), 5830 (GH), 5831 (GH, US), 5832 (GH), 5840 (GH, US), 5841 (GH), 5842 (GH), 5843 (GH), 5844 (COL, GH, P), 5845 (GH, F, US), 5846 (GH), 5848 (BM, GH), 5849 (GH), 5860 (GH), 5862 (GH, NY, P), 5863 (GH, LE), 5864 (GH), 5865 (B, GH), 5878 (GH); Vareschi 6978b (VEN); Vareschi & Lasser 389 (VEN); Vareschi & Pannier 941 (US, VEN), 1279 (VEN), 1430 (US, VEN), 1729 (VEN). TACHIRA: Archer 3153 (US); Páramo de Tamá, Cardona 306 (US, VEN); Müller 1017 (VEN); Páramo de la Negra, Tryon & Tryon 5884 (BM, COL, F, GH, US), 5886 (B, GH, P, NY). COLOMBIA. NORTE DE SANTANDER: Páramo de Tamá, Cuatrecasas, et al. 12606 (GH, US).

Variant with sparse tomentum, small pinnae and usually bent pinna stalks: VENEZUELA. MERIDA: Páramo de Timotes, Alston 6600 (BM,

GH), 6654 (BM, GH), Páramo de Mucuchies, Barclay & Juajibioy 9702 (GH), Páramo de Mucubaji, 9812 (GH); Gines 1744 (US); Páramo de Conejos, Hanbury-Tracy 104 (K); Jahn 162 (US), Páramo Quinora, 725 (US, VEN); Mägdefrau 561 (GH, U); Pittier 13184 (G, US, VEN), 13247 (US, VEN); Tryon & Tryon 5829 (GH), 5834 (F, GH, US), 5847 (GH, US), 5850 (BM, GH, NY, US), 5851 (GH), 5853 (GH, US).

9. Jamesonia Scammanae A. F. Tryon, sp. nov. Fig. 9. Map 9

Trichomata rhizomatis plerumque appressa vel laxa, patentia, pallida usque obscuro-fusca, laminae angustae 2-6 mm. latae, gemma vermiformis, glutinosa, rachis glutinosa, crustosa, pinnae ovatae vel lobatae, subsessiles vel petiolulis ad 0.7 mm. longis, pinna adaxialiter vernicosa vel crustosa, abaxialiter tomentosa, trichomatibus crispatis, albidis vel fulvis, limbo modice lato, integro vel leviter undulato, sporae pallide succineae vel fulvae, laeves.

TYPUS: Costa Rica, Cerro de la Muerte, March 25, 1956, Edith Scamman and L. R. Holdridge 7929 GH.

Rhizome long creeping, dichotomously branching, slender ca. 1-2 mm. in diameter with sparse roots, the internodes variable in length, the trichomes usually rigid, appressed, sometimes lax, patent, lustrous light to dark brown, usually darker than the rhizome surface, 1.0-1.5 mm. long with usually 1 (-5) cells near the base, apex acuminate. Petiole often bent or curled near the rhizome, sometimes appressed, 3-11 cm. long, about 1/9 to 1/3, rarely 1/2 as long as the lamina, atropurpureus, in old leaves often blackish and crustose, terete or somewhat ellipsoidal, ca. 0.75-1.0 mm. in diameter at the apex, filiform below, the trichomes sparse, brown or bicolorous with clear cells at the base, apical cells acuminate. Lamina once pinnate, ca. 11-45 cm. long, ca. 0.2-0.6 cm. wide, about the same size throughout with the base slightly narrowed, ca. 70-300 pinnae, indeterminate, the apical bud vermiform, usually larger than the mature pinnae, glutinose with appressed trichomes. Rachis similar in color to the petiole, terete, ellipsoidal or trigonous the upper surface with an obtuse angle, glutinose or crustose, the trichomes more abundant on the lower surface, generally longer adjacent to the pinnae but not exceeding them in length, clear or tan, the apical cell bulbous or sometimes acuminate. Pinnae alternate or subopposite, approximate or distant, in 2 ranks sometimes overlaying the rachis, (basal ones smaller, distant, sterile, usually persistent) ovate, sometimes lobed, usually with a central furrow on the upper surface, the margins enrolled, inequilateral at the base, 1.5-4.0 mm. long, 1.5-3.0 mm. wide, gray or bright green, rigid herbaceous; upper surface vernicose or crustose with short, appressed glands, the epidermal cell walls unthickened; lower surface tomentose with whitish or tan, crispate trichomes of one or few cells, stalk bent, ca. 0.25-0.75 mm. long, atropurpureus, not articulate, pinnae usually subsessile. Veins broad to moderately broad, more or less sunken on the upper surface, dichotomous with branches at wide angles, the branches moderately long, the ends clavate or flabellate extending into the border. Border moderately broad, firm-membranous or similar to the pinna in texture, entire or slightly undulate, opaque white or

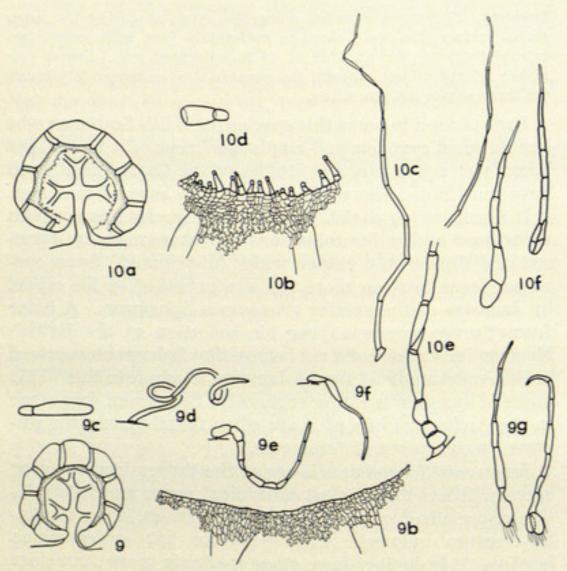
lutescent. Sporangia crowded along the veins, obscuring the lower pinna surface, the stalk short to moderately long with some intercalary divisions, the annulus of 19-23 indurated cells. Spores pale amber colored or tan, smooth, the equatorial wing moderately broad, the three angles not projecting.

I am pleased to name this species for Edith Scamman who has collected complete and ample specimens of it from Costa Rica. Her collections and studies of the Costa Rican ferns have contributed appreciably to our knowledge of that area.

It is surprising that this distinctive species has not been recognized earlier for collections of it were made by Jameson and Spruce and rather widely distributed. Some correspondence between these two was provoked by the report by Jameson of the species growing in Sphagnum. A letter from Spruce accompanying his collection at the British Museum indicates he did not believe that Sphagnum occurred in the Andes and had forced Jameson to admit to this. This abuse of Jameson is rather curious for Sphagnum does occur in the Andes and bits of it are often found among the rhizomes in collections of Jamesonia.

Jamesonia Scammanae is one of the three widest ranging species; it has the greatest altitudinal range and it is relatively specialized in its shortened pinna stalks, in the glandular-crustose indument and elaborate but entire pinna borders. It is distinct from other species in these characters and in the glutinose, vermiform leaf buds although there is a general resemblance to J. imbricata var. glutinosa in the small, widely spaced, glutinose pinnae. In several more detailed characters of the pinnae as the broad veins, which are dichotomous at wide angles, the central furrow on the upper surface, the cordate base, and especially in the dense, crispate trichomes on the lower surface and in the light colored spores there is a greater resemblance to J. bogotensis.

Central Bolivia to Costa Rica, at 1830-4300 m. Additional specimens examined: COSTA RICA. Carson, in 1956 (GH). CARTAGO: Cerro de la Muerte, Carpenter 289 (US); Holm & Iltis 476 (B, BM, S-PA, US); Cerro de Buena Vista, Pittier & Tonduz 3350 (B, BM, P, US); Rogers CR25 (GH); Scamman 6078 (GH), 6078B (GH), 7052 (GH); Williams CR25 (US). SAN JOSE: Dos Burros Peaks, Dayton 3083 (US); Cerro de las Vueltas, Standley 43842 (US), 43875 (US). COLOMBIA. CALDAS: Páramo de Las Letras, Barclay & Juajibioy 6280 (GH); Páramo DAS: Páramo de Las Letras, Barclay & Juajibioy 6280 (GH); Páramo Ruiz, Tryon & Tryon 6142 (GH). CAUCA: Páramo de Puracé, Tryon & Tryon 5960 (COL, GH), 5980 (GH). TOLIMA: Páramo de Herveo, Hantryon 5960 (COL, GH), 5980 (GH). TOLIMA: Páramo de Herveo, Hantryon 5960 (COL, GH), 5980 (GH). TOLIMA: Páramo de Herveo, Hantryon 5960 (COL, GH), 5980 (GH). TOLIMA: Páramo de Herveo, Hantryon 5960 (COL, GH), 5980 (GH). TOLIMA: Páramo de Herveo, Hantryon 5960 (COL, GH), 5980 (GH). TOLIMA: Páramo de Herveo, Hantryon 5960 (COL, GH), 5980 (GH). TOLIMA: Páramo de Herveo, Hantryon 5960 (COL, GH), 5980 (GH). TOLIMA: Páramo de Herveo, Hantryon 5960 (COL, GH), 5980 (GH). TOLIMA: Páramo de Herveo, Hantryon 5960 (COL, GH), 5980 (GH).



Figs. 9 and 10. Fig. 9. J. Scammanae: a, pinna, × 10, from Scamman & Hold-ridge 7929 (gH); b, pinna margin with two vein ends, × 35, from Vargas 1060 (gH); c, gland from upper pinna surface, enlarged; d, trichome from lower pinna surface, × 40; the last two from Asplund 9922 (gH); e, rachis trichome, × 30, from Cook & Gilbert 1833 (us); f, petiole trichome, × 30; g, rachis trichomes, × 30; the last two from Scamman 6078 (gH). Fig. 10. J. peruviana: a, pinna, × 10; b, pinna margin with two vein ends, × 35; the last two from Pennell 13873 (gH); c, trichome from upper pinna surface, × 30, from Macbride 4404 (F); d, gland from lower pinna surface, enlarged, from Pennell 13873 (gH); e, rachis trichome with five cells omitted from the mid-portion, × 30; f, rhizome trichomes, × 30; the last two from Macbride 4404 (F).

CARCHI: Páramo del Angel, Barclay & Juajibioy 9410 (GH); Fagerlind & Wibom 1509 (S). IMBABURA: Wiggins 10420 (US). PICHINCHA: Antitana, Jameson (B, BM, G, GH), Guamini, Jameson 768 (BM, E, K); Spruce 5660 (BM, G, K, LE, P). TUNGURAHUA: Cord. de Llanganates, Asplund 9922 (GH, S). PERU. Lechler 2032 (B, E, K, LE, P). APURIMAC: Santander et al in 1935 (UC); Vargas 1060 (GH). CUZCO: Bües 1008 (US); Cook & Gilbert 1242 (US), 1833 (US); Cerro de Cusilluyoc, Pennell 13870 (F, GH, US); Paucartambo, Soukup 386 (F); Vargas 11165 (F, K, UC). HUANUCO: Macbride & Featherstone 2182 (F, GH, US). JUNIN: Bryan 183 (F, US); Kunkel 485 (GH). LIMA: Saunders 399 (BM). BOLIVIA. COCHABAMBA: Cárdenas 668 (GH, US); Herzog

789 (US). LA PAZ: Asplund 1074 (BM, S-PA); Mandon 1552 (BM, GH, K, LE, P); Rusby 141 (GH, US); Pongo, Tate 111 (US).

10. Jamesonia peruviana A. F. Tryon, sp. nov. Fig. 10. Map 10

Trichomata rhizomatis rigida plus minusve appressa, castanea vel atropurpurea, apex laminae indeterminata, gemmae tomento fulvo vel stramineo, pinnae imbricatae, reniformes vel orbiculares, rigide herbaceae vel leviter coriaceae, pinna adaxialiter tomentosa trichomatibus longis, sapienter paucim pinnas circumjectis, abaxialiter trichomatibus brevibus, capitatis, nervis latis, dichotomis, angulis latis marginem non attingentibus, limbo lato, papillis plus minusve uniformibus, sporae fulvae vel stramineae, leviter papillatae.

TYPUS: Peru, Huanuco, Tambo de Vaca, 13,000' J. F. Macbride 4404,

F; isotypus, Us.

Rhizome long creeping, dichotomously branched, slender, ca. 1.0-1.5 mm. in diameter with moderately dense, delicate roots, the internodes variable in length, the trichomes rigid, more or less appressed, castaneus or atropurpureus, darker than the rhizome surface, ca. 1.0-1.5 mm. long, with 1 or 2 cells at the base, apex acuminate. Petiole usually bent and somewhat appressed to the rhizome for a short distance before ascending, 1-3 cm. long, possibly longer, 1/27, 1/14 as long as the lamina, castaneus, terete, ca. 0.5-1.0 mm. in diameter at the apex about the same size throughout, with sparse, clear trichomes. Lamina once pinnate, ca. 17-40 cm. long, 0.3-0.5 cm. wide, broadest at the apex, narrower toward the base, with ca. 250-600 pinnae, indeterminate, the apical bud larger than the mature pinnae, with trichomes patent or somewhat appressed. Rachis castaneus, often slightly lighter colored than the petiole, ellipsoidal, or trigonous and the upper surface with an obtuse angle, tomentose, the trichomes long, two or more times longer than the pinnae, discrete, tan or straw colored, with the lower cells clear, the apical cell bulbous, rarely acuminate. Pinnae subopposite, usually stacked in 2 ranks, imbricate, deciduous, (the basal ones, minute and distant or often absent) reniform or orbicular-cordate, concave on the upper surface, the margin enrolled, inequilateral at the base with the acroscopic lobe often larger and bent, 1.5-2.5 mm. long, 2-3 mm. wide, yellow-green, rigid herbaceous or slightly coriaceous; upper surface with long, discrete, gold colored trichomes, strongly bent near the base of the trichome, appressed and usually enveloping several pinnae, the epidermal cell walls sometimes slightly thickened; lower surface with sparse, short, 1 or 2 celled, capitate trichomes and a tuft of longer, tan or clear trichomes on the stalk and adjacent veins, sometimes somewhat pubescent along all veins, stalk straight, ca. 0.75 mm. long, tan, frequently articulate. Veins broad, slightly sunken especially on the upper surface near the stalk, dichotomous with wide angles, the branches short or moderately long, the ends clavate or nearly acute, extending to the border. Border broad, firm membranous with more or less uniform papillae or cilia, tan or rust colored. Sporangia usually few on veins adjacent to the stalk, sometimes obscuring the lower surface, short stalked with many intercalary cell divisions, the annulus of 16-23 indurated cells. Spores tan or straw colored,

papillose or sparsely verrucose, the equatorial wing moderately broad, the 3 angles prominently projecting.

The species is unique in having, on the upper surface of the pinnae, long, appressed but discrete trichomes which cover several pinnae, and a fringe of fairly uniform cilia or papillae along the pinna border. The northernmost collection from Libertad differs from the others in having acuminate rather than bulbous tipped rachis trichomes and fairly dense pubescence on the lower pinna surface. Some collections are mixed with Jamesonia scalaris and with J. Alstonii and there is a resemblance between the latter and J. peruviana in the stacked alignment of the pinnae on the rachis and the ciliate pinnae margins. There is also a resemblance to J. rotundifolia in the long, gold colored trichomes on the upper pinnae surface. I have seen only two rhizomes and they are probably difficult to collect for the plants are reported to grow among grasses in boggy places.

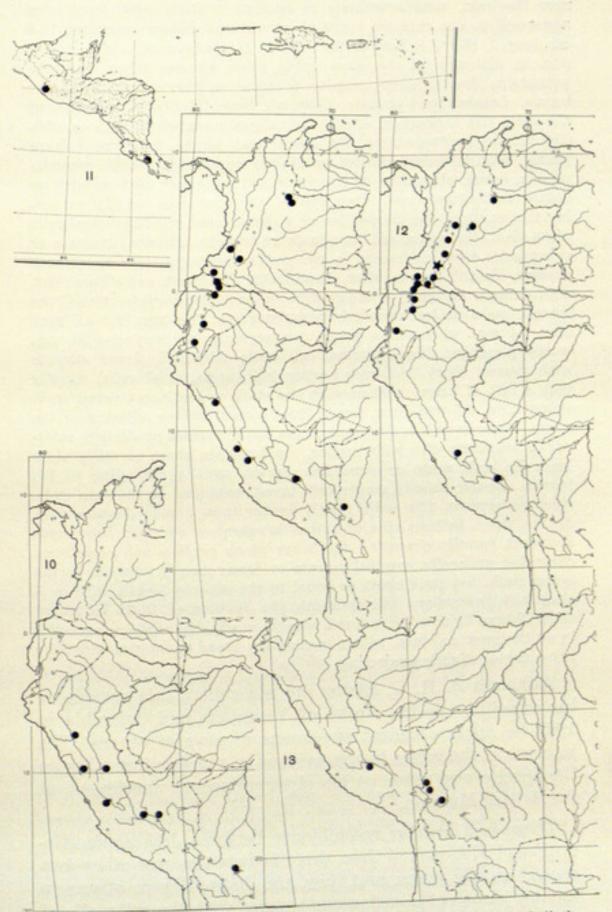
The collections are from Peru with the exception of one specimen from central Bolivia, reported from 2900 m. which is the lowest altitude for the species. The Peruvian material ranges from 3400-4300 m. Additional specimens examined: PERU. Domby 18 (G, L, P); Lechler 2153 (G); Née (F); Pavon 137 (G). ANCASH: Weberbauer 3302 (B, G, US). CUZCO: Bües 1530 (US), 1531 (US), 1598 (US), 2161 (US); Pennell 13873 (F, GH, US). HUANUCO: Bryan 648 (F, US); JUNIN: Macbride & Featherstone 1883 (F, G, GH, US); Pearce, in May 1863 (K). LA LIBERTAD: Lopez & Sagástegui 3346 (GH). BOLIVIA. COCHABAMBA: Brooke 6196 (U, US).

11. Jamesonia Alstonii A. F. Tryon, sp. nov. Fig. 11. Map 11

Trichomata rhizomatis rigida, appressa, pallida usque obscurofusca vel nigricantia, laminae 0.4-1.0 cm. latae, latitudum prope uniformum, rhachis et gemma tomento fulvo vel stramineo, pinnae ovatocordatae vel orbiculato-cordatae, coriaceae, pinna adaxialiter glabra, infrequens glandulosa, abaxialiter trichomatibus parce bulbosis, nervis latis, dichotomis, angulis latis, marginem non attingentibus, limbo lato vel modice lato, cretaceo vel luteo-albido irregulariter dentato, integro vel ciliis brevibus bulbosis, sporae pallidae succineae, leviter verrucosae.

TYPUS: Colombia, Depart. del Valle, Cordillera Occidental, Los Farallones, vertiente oriental, bajo el filo de la Cordillera en el cerro de La Torre: La Laguna, 3500-3550 m. Aug. 1, 1945, J. Cuatrecasas 21884, GH; isotypi: COL, US.

Rhizome usually long creeping, sometimes compact, dichotomously branched, ca. 2.0-3.5 mm. in diameter with moderately dense, long roots, the internodes variable in length, the trichomes rigid, appressed, sometimes light brown, usually dark brown or blackish, darker than the rhizome surface, ca. 1.5-2.5 mm. long, with usually 1 (-4) cells

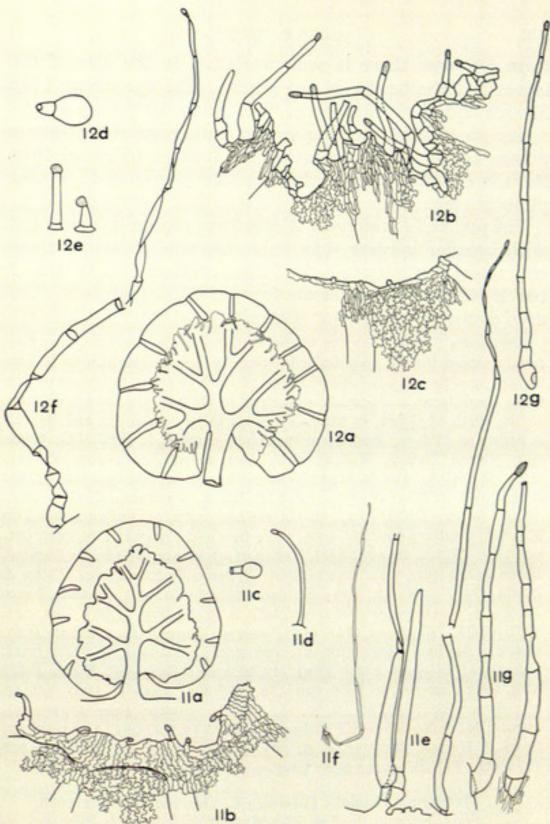


Maps 10-13. Map 10, J. peruviana. Map 11, J. Alstonii. Map 12, J. Goudotii, the star at the locality of the variant, hybrid collection. Map 13, J. boliviensis.

near the base, apex acuminate or bulbous. Petiole bent, sometimes appressed to the rhizome for a short distance before ascending, 2-6 cm. long, 1/10-1/5 as long as the lamina, atropurpureus, terete, ca. 1-2 mm. in diameter at the apex, often more slender below, sparsely pubescent, the trichomes similar to those of the rachis or darker brown. Lamina once pinnate, 15-40 cm. long, 0.4-1.0 cm. wide, about the same size throughout or the base slightly narrowed, with ca. 100-450 pinnae, indeterminate, the apical bud larger than the mature pinnae, with trichomes matted or slightly appressed. Rachis atropurpureus, terete, ellipsoidal or trigonous and the upper surface with an obtuse angle, tomentose, often matted, the trichomes usually exceeding the length of the pinnae, tan or straw colored, with the basal cells often clear, the apical cell acuminate or bulbous. Pinnae alternate or subopposite, usually stacked in two ranks, imbricate, (the basal ones smaller, distant, sterile, often deteriorated or absent, sometimes, flat, with dentate margins) ovate-cordate or orbicular-cordate, plane, the margin more or less enrolled, inequilateral at the base, 3.5-4.5 mm. long, 2-5 mm. wide, yellow-green, coriaceous; upper surface glabrous, rarely glandular, the epidermal cell walls thickened; lower surface with sparse, short trichomes having bulbous terminal cells, usually with a tuft of longer trichomes on the stalk and adjacent veins, stalk straight, ca. 0.5 mm. long, tan to light brown, lighter adjacent to the pinna. Veins broad, in the plane of the upper surface or slightly sunken, dichotomous with wide angles, the branches short or moderately long, the ends acute or somewhat clavate, usually extending to the border. Border usually moderately broad, extended at the vein ends, rigid herbaceous, (the cells mostly longer than broad) dentate with sparse, short, bulbous cilia or entire, lutescent or whitish. Sporangia abundant, usually obscuring the lower pinna surface and sometimes extending under the enrolled margin or fewer mostly adjacent to the pinna stalk, the stalk short or equal to the capsule length, of 2 or 3 tiers with intercalary cell divisions, the annulus of 15-22 indurated cells. Spores light amber colored, smooth or slightly papillose especially on the proximal face, with a moderately broad equatorial wing, the three angles slightly projecting.

Although A. H. G. Alston did not collect this species on his expedition to the Andes of Venezuela and Colombia in 1939 he made excellent specimens of several others. His interest in the genus is also evident in a preliminary key to the species and notes on his observations on specimens, at the British Museum.

There is a greater resemblance between Jamesonia Alstonii and J. Goudotii than there is between any other two species in the genus and they are distinct from others in having pinnae of a coriaceous texture with the cell walls of the upper epidermis thickened. Considering its extensive distribution, J. Alstonii is morphologically relatively uni-



Figs. 11 and 12. Fig. 11. J. Alstonii: a, pinna, × 10, from Cuatrecasas 21884 (gH): b, pinna margin with three vein ends, the heavy lines indicating a fold in the tissue. × 35, from Asplund 16886 (gH): c, gland from the upper pinna surface, enlarged, Stork & Horton 10007 (F): d, capitate trichome from lower pinna surface, × 30: e, rachis trichomes, the right one with four cells omitted from the mid-portion, × 30: f, petiole trichome, × 30: the last three from Cuatrecasas 21884 (gH): g, rhizome trichomes, × 30, from Killip & Smith 17475 (gH). Fig. 12. J. Goudotii: a, pinna, × 10, from Cuatrecasas 19110 (gH): b, pinna margin with two vein ends, × 35, from Mexia 7552 (gH): c, pinna margin with two vein ends, × 35, from Penland & Summers 814 (US): d, gland from upper pinna surface, enlarged, from Asplund 9942 (gH): e, capitate trichomes from lower pinna surface, × 45, from Cuatrecasas 20303 (gH): f, rachis trichome with six cells omitted from the mid-portion, × 30: g, rhizome trichome, × 30, from Asplund 8779 (gH).

form although there is some variation in the size of the leaves and the border of the pinnae. The specimens from Mexico and Costa Rica may have a few trichomes on the upper surface of the pinnae and rather narrow, dentate pinnae borders. The collection of Stork and Horton from Peru is exceptional in having capitate glands on the upper pinna surface.

The pinnae in Jamesonia Alstonii are generally longer and with broader borders than in J. Goudotii although these characters may vary in each of these species. The bicolorous rachis tomentum and clavate form of the lamina in J. Goudotii distinguish it from J. Alstonii.

Jamesonia Alstonii has the widest distribution in the genus ranging from western Bolivia near Lake Titicaca to Chiapas, Mexico on Volcan Tacaná and has an altitudinal range of 2850-4200 m. It occurs on the three Cordilleras in Colombia, occurring at 2890 m. the lowest altitude in the south of Colombia while in the north in Santander and Boyaca it occurs at 4200 m. Additional specimens examined: MEXICO. CHIA-PAS: Volcán Tacaná, Matuda S-234 (GH, K, US), 2864 (GH, K, US). GUATEMALA. SAN MARCOS: Volcán Tajumulco, Sharp 46113 (US); Steyermark 36114 (GH, US). COSTA RICA. CARTAGO: Carlson 3516 (GH); Rogers CR24 (GH). COLOMBIA. BOYACA: Páramo del Alto Escobal, Cuatrecasas 1766 (COL, US); Grubb & Guymer P36 (BM, COL, GH, US). CAUCA: Haught 5101 (COL, US). NARINO: Volcán de Cumbal, Ewan 16133 (GH, US). SANTANDER: Páramo de Santurbán, Killip & Smith 17475 (COL, GH, US); St. John 20772 (GH, US). VALLE: Cerro La Torre, Cuatrecasas 17859 (GH, US), Alto del Buey, 17963 (GH, US). ECUADOR. Espinosa 2217 (US). CANAR: Rose & Rose 22755 (US). CARCHI: Asplund 16886 (GH, S). COTOPAXI: Couthouy, in 1855 (GH). IMBABURA: Wiggins 10286 (US). PICHINCHA: Guamani, Ewan 16437 (GH, US); Jameson, in 1856 (GH), in 1857 (G); Mille 41 (US), 172 (P, U); Spruce 5659 (B, BM, G, K, P). PERU. CUZCO: Bües 1378 (US), JUNIN: Mito, Macbride & Featherstone 1883 (B, GH, US). LA LIBERTAD: Stork & Horton 10007 (F, G, K, UC). PASCO: Huayllay, Mathews 979 (E, G, K). BOLIVIA. LA PAZ: Cárdenas 1025 (GH).

Jamesonia Goudotii (Hieron.) C. Chr. Ind. Fil. 373. 1905. Fig. 12. Map 12

Gymnogramma Goudotii Hieron. Engl. Bot. Jahrb. 34: 476. 1904. TYPE: Goudot, Colombia B!, photos: col., F, GH, NY, US; isotypes G! P!. Rhizome long creeping, dichotomously branched, 1.5-4.0 mm. in diameter with moderately dense to dense, long roots, the internodes variable in length, the trichomes rigid, appressed, light brown to lustrous black, darker than the rhizome surface, ca. 2-3 mm. long, with usually 1 (-3) cells near the base, apex bulbous often exuding. Petiole usually bent and somewhat appressed to the rhizome for a short distance before ascending, ca. 0.5-21 cm. long, 1/20 to nearly equal the length of the lamina, atropurpureus, terete or oval ca. 1-3 mm. in

diameter at the apex, the same size throughout, sparsely pubescent with trichomes similar to those of the rachis. Lamina once pinnate, 5-40 cm. long, 0.5-1.2 cm. wide, broadest at the apex narrowed toward the base, with ca. 50-350 pinnae, the central portion rarely broadest, indeterminate, the apical bud usually larger than the mature pinnae, with trichomes erect or slightly appressed. Rachis similar or lighter colored than the petiole, terete, ellipsoidal or trigonous and the upper surface with an obtuse angle, rarely channeled, tomentose, the trichomes up to twice as long as the pinnae, bicolorous usually clear in the basal portion, brown above, the apical cell usually bulbous, sometimes acuminate. Pinnae alternate, subopposite, usually stacked in 2 ranks, imbricate, (the basal ones smaller distant, sterile, finally deciduous or sometimes persistent) reniform, orbicular-cordate or longovate and auriculate, plane, the margin incurved, sometimes strongly so, forming a pouch-like structure, inequilateral at the base 3-8 mm. long, 3-7 mm. wide, light or yellow-green, coriaceous; upper surface usually glabrous, sometimes glandular, rarely pubescent with light tan or bicolorous trichomes the epidermal cell walls thickened; lower surface with sparse, short, bulbous, clear or tan trichomes on the veins, with a tuft of longer trichomes on the pinna stalk and adjacent veins, stalk straight, ca. 1.0 mm. long, tan or slightly darker, always lighter colored adjacent to the pinnae. Veins broad, in the plane of the upper surface or slightly sunken, dichotomously branched at wide angles, the branches moderately long, the ends clavate or flabellate, extending to or nearly to the margin. Border irregularly dentate, usually extended at the vein ends rarely entire or nearly so, (the cells mostly broader than long) usually ciliate, the cilia with the terminal cell bulbous and sometimes bicolorous, rigid herbaceous, clear, whitish or lutescent. Sporangia abundant sometimes obscuring the lower surface and extending under the incurved margin, the stalk from 1/2 as long to equal the capsule length, the lowest tier sometimes thickened and dark brown, the annulus of 17-21 indurated cells. Spores tan or light amber colored, usually papillose to verrucose, with a broad, sometimes crenate or irregularly lobed equatorial wing, the 3 angles broad, slightly projecting; rarely large and shriveled.

The close relationship between this and J. Alstonii is evident in the form, indument, border and particularly in the texture of the pinnae. There are two collections from Páramo de las Papas, in southern Colombia, near Valencia which resemble J. Goudotii in having ruddy brown tomentum on the rachis, irregularly dentate and ciliate borders and coriaceous pinnae. However, the pinnae are auriculate with whitish trichomes on the upper surface, the rachis is slightly channeled and the spores are exceptionally large and irregular. This material appears to be intermediate between Gymnogramma Mathewsii var. glabriuscula and J. Goudotii. Specimens of the former were mixed in one of the collections

of the intermediate. Jamesonia Goudotii has also been collected on this paramo.

A specimen of *J. Goudotii*, from the market in Huancayo, Peru, was sent to me by *G. Kunkel*, 486.

Jamesonia Goudotii has a similar but more limited range (from southern Peru to northern Colombia) than J. Alstonii and has a slightly higher altitudinal range of 3000-4700 m. Additional specimens examined: COLOMBIA. Bordoncillo, Lehmann 529 (B, BM, G, K, LE, P, US). ANTIQUIA: Mayor 68 (S-PA, US). BOYACA: Bischler 2760 (COL). CALDAS: Bischler 1491 (COL); Barclay & Juajibioy 6354 (GH); Cuatrecasas 9232 (GH); Páramo del Quindio, Pennell & Hazen 9932 (GH, US). CAUCA: Cuatrecasas 19110 (GH, US); Páramo de Moras, Pittier 1388 (US). CUNDINAMARCA: Guadalupe, Haught 5072 (S-PA, US). HUILA-CAUCA: Páramo de las Papas, Idrobo, et al. 3107 (COL, GH). NARINO: Volcán de Chiles, Ewan 16003 (GH, US), Páramo of Cerro San Francisco, 16246 (GH, US). SANTANDER: Almorzador, Vareschi 4038 (VEN). TOLIMA: Páramo de Hervo Fresno, Hanbury-Tracy 627A (K); Páramo de Ruiz, Pennell 3040 (GH, US). VALLE: Páramo de Las Vegas, Cuatrecasas 20303 (GH, US). ECUADOR. AZUAY: Jameson 119 (K); Steyermark 53073 (US). CHIMBORAZO: Páramo de La Laguna Negra, Barclay & Juajibioy 8775 (GH). IMBABURA: Penland & Summers 814 (F, US); Sodiro 4/92 (K). NAPO-PASTAZA: Asplund 8779 (GH, s); Barelay & Juajibioy 9100 (GH). PICHINCHA: Ewan 16440 (GH, U, US). TUNGURAHUA: Asplund 9942 (GH, S); Rimbach 43 (L, P, S-PA, US). PERU. CUZCO: Bües 1406 (US). JUNIN: Weberbauer 6629 (F, GH, US).

Intermediate specimens: COLOMBIA. HUILA-CAUCA: Páramo de las Papas, Idrobo, et al. 3108 (COL), 3336 (COL, GH).

13. Jamesonia boliviensis A. F. Tryon, sp. nov. Fig. 13. Map 13

Trichomata rhizomatis rigida, appressa, atropurpurea vel nigricantia, apex laminae indeterminata gemmae tomento patente, fulvo vel rufo-fusco, pinnae imbricatae, orbiculato-cordatae vel ovato-cordatae, inequilaterales, planae, rigidae herbaceae, epidermis supra cellulis subcrassioribus, pinna adaxialiter et abaxialiter trichomatibus glandulosis brevibus nervis ultra marginem protrusis, limbo angusto, ciliis glandulosis, sporae pallidae, succineae, papillatae.

TYPUS: Peru, Dept. Apurimac, Bosques de Ampay, 3200 m. June 1938, C. Vargas 1060a, GH; isotypus: US.

Rhizome long creeping, dichotomously branched, ca. 1.5-2.5 mm. in diameter with sparse roots, the internodes variable in length, the trichomes rigid, appressed, lustrous atropurpureus or blackish, darker than the rhizome surface, 1-2 mm. long, 2 or usually 1 cell at the base, apex bulbous or decapitated. Petiole bent, appressed to the rhizome for a short distance before ascending, 1.0-7.5 cm. long, about 1/8 to 1/5 as long as the lamina, atropurpureus, terete, ca. 0.5-1.0 mm. in diameter at the apex, often more slender below, with short capitate trichomes and longer trichomes similar to those of the rachis. Lamina once pinnate, 9-30 cm. long, 0.3-0.7 cm. wide, about the same size

throughout or the base slightly narrower, with ca. 100-225 pinnae, indeterminate, the apical bud the same size or slightly larger than the mature pinnae, with patent trichomes. Rachis castaneus, terete or trigonous and the upper surface with an obtuse angle, pubescent or tomentose, and sometimes matted on the lower surface, the trichomes as long or slightly longer than the pinnae, rust-brown, with the basal cells often clear, the apical cell bulbous or acuminate. Pinnae alternate, subopposite, in 2 ranks laterally disposed, imbricate, (the basal ones smaller, often incompletely developed, distant, sometimes persistent) orbicular-cordate or ovate-cordate, plane, the margin incurved, inequilateral at the base, 2-4 mm. long, 2-4 mm. wide, bright or yellow green, rigid herbaceous; upper and lower pinna surfaces with short, capitate trichomes, the latter with longer trichomes on the stalk and adjacent veins, the cell walls of the upper epidermis slightly thickened, stalk straight, ca. 0.5 mm. long, atropurpureus, lighter adjacent to the pinnae. Veins broad, in the plane of the upper surface or slightly raised or sunken, dichotomous with wide angles, the branches short or moderately long, the ends acute or clavate, protruding from the margin. Border narrow, a row of cells mostly broader than long, with capitate cilia. Sporangia abundant, obscuring the lower pinna surface or fewer and mostly adjacent to the pinna stalk, the stalk short, about 1/4 the capsule length, with 2 tiers, the lower with intercalary cell divisions, the annulus with 18-24 indurated cells. Spores light amber colored, papillose, the equatorial wing broad, the 3 angles slightly projecting.

This species has been obscure since most of the collections of it are mixed with other species as Jamesonia scalaris, J. Scammanae, J. blepharum and with Eriosorus elongatus. The fine collection of César Vargas is the most complete and ample material.

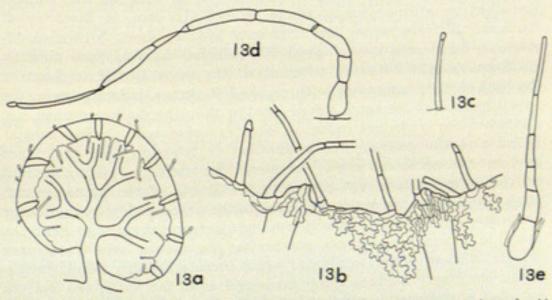


Fig. 13. J. boliviensis: a. pinna, X 10; b. pinna margin with two vein ends, X 35; c, capitate trichome from lower pinna surface, enlarged; d, rachis trichome, X 30; e, rhizome trichome, X 30; all from Vargas 1060a (GH).

It is a distinctive species and remarkable for the genus in having a single kind of capitate trichome or cilia on each of the pinna surfaces and the margin. Such uniformity of indument does occur in species of *Eriosorus* but in the other species of *Jamesonia* there has been specialization of the pinna indument.

The collection from Peru is from the lowest altitude at 3200 m. and the other collections from northern Bolivia are from 3400 and 4200 m. Additional specimens examined: PERU. APURIMAC: Santander, et al. in Oct. 1935 (UC). BOLIVIA. LA PAZ: Unduavi, Buchtien 2733 (US); Cárdenas 1025 (GH), 1026 (GH); Pelechuco, Pearce in 1865 (K); Tolapampa, R. S. Williams 1152 (US), 1153 (GH, US), Pelechuco, 2628 (US).

Jamesonia scalaris Kunze, Bot. Zeit. 2: 738. 1844. Fig. 14. Map 14

TYPE: Ruiz 49, Peru, Pillao B!, photos COL, F, GH, NY, US; isotypes HAL, P! US!.

Gymnogramma scalaris (Kunze) Kl. Linnaea 20: 407. 1847.

Psilogramme scalaris (Kunze) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 334. 1882.

Jamesonia imbricata (Sw.) Hook. and Grev. var. scalaris (Kunze) Sodiro, Crypt. Vasc. Quit. 387. 1893.

Rhizome wide creeping, dichotomously branched, ca. 1.5-2.0 mm. in diameter with moderately dense roots, the internodes variable in length, the trichomes rigid, appressed or somewhat patent, light to dark brown or atropurpureus, about the same color as the rhizome surface or slightly darker, 1.5-2.0 mm. long usually with 2 (-5), cells near the base, apical cell bulbous, exuding. Petiole bent or curled near the rhizome, usually appressed to the rhizome for a short distance before ascending 2.5-6.5 cm. long, 1/16-1/5 as long as the lamina, castaneus or atropurpureus, terete, ca. 0.75-1.0 mm. in diameter at the apex, filiform below, the trichomes sparse, short, brown or bicolorous, basal cells clear, apical cell bulbous. Lamina once pinnate, 10-33 cm. long, 0.2-0.6 cm. wide, about the same size throughout or the base slightly narrowed, with ca. 50-270 pinnae, indeterminate, the apical bud about the same size or smaller than the mature pinnae, not glutinous, the trichomes patent or slightly appressed. Rachis similar in color to the petiole, terete, elliptical or trigonous and the upper surface with an obtuse angle, pubescent, the trichomes more abundant on the lower surface, not exceeding the length of the pinnae, clear, tan or bicolorous, the upper cells darker, the apical cell bulbous. Pinnae alternate, approximate, usually not imbricate or slightly so near the apex, in 2 ranks sometimes overlaying the rachis, (the basal ones minute, distant, often persistent) ovate-cordate, usually lobed, patelliform, the upper surface often depressed near the stalk, the margin enrolled, equilateral or nearly so at the base, 2-4 mm. long, 1.5-3.0 mm. wide, bright green, herbaceous; upper surface with papillate glands, the epidermal cell walls unthickened; lower surface with 1 or few

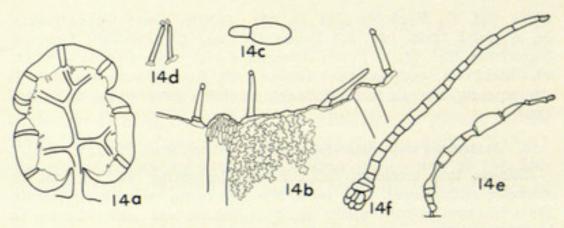


Fig. 14. J. scalaris: a, pinna, X 10, from Asplund 13718 (GH); b, pinna margin with two vein ends, X 35; c, gland from upper surface of pinna, enlarged; d, capitate trichomes from lower pinna surface, enlarged; the last three from Bücs 2163 (US); e, rachis trichome, X 30 from Asplund 13718 (GH); f, rhizome trichome, X 30, from Bües 2163 (US).

celled, erect, clear, capitate trichomes, sometimes tomentose, usually with a tuft of clear trichomes on the stalk or adjacent veins, stalk straight or slightly bent, ca. 0.75-1.50 mm. long, atropurpureus, usually lighter adjacent to the pinna, articulate in older leaves. Veins slender or moderately broad, in the plane of the upper surface or raised, dichotomous with wide angles, the branches short or moderately long, the ends clavate or somewhat acute, extending to the margin or protruding. Border narrow, a row of cells broader than long, with capitate cilia. Sporangia mostly adjacent to the pinna stalk, the stalk short or moderately long, of 2 or 3 tiers with intercalary cell divisions, the annulus of 17-20 indurated cells. Spores dark brown, smooth or slightly verrucose especially on the distal face, the equatorial wing narrow, the 3 angles prominently projecting.

Jamesonia scalaris was the first to be described among the species with small pinnae and subsequently the name has been applied to most specimens of that form. The species is quite distinct in the lobed and patelliform pinnae with glands on the upper surface and narrow, ciliate borders. The basal pinnae of the lamina are sometimes minute with stalks up to twice as long as the pinnae and the amount of indument on the lower surface of the pinna may vary from sparse to dense. It has been collected with J. peruviana, J. Scammanae and J. brasiliensis and resembles the last in the symmetrical form of the pinnae, the dark spores, and the narrow, ciliate pinnae borders. In the last character it is also similar to J. boliviensis.

It occurs from central Peru to northern Bolivia, at 2300-4700 m. Additional specimens examined: PERU: Hill 553 (K). CUZCO: Bües 1533 (US), 1783 (US), 1784 (US), 1787 (US), 1931 (US), 2161 (US), 2163 (US), 2190 (US); Marcapata, Stafford 989 (K); Paucartambo, Vargas, in June 1937 (GH). HUANUCO: Punta de Panao, Asplund 13718 (GH, S), Macbride 4524 (F, US). JUNIN: Cerró Goyllarisquisca, Asplund 11922 (GH, S); Pavon 137 (G). LA LIBERTAD: Lopez & Sagástegui 3435 (GH). PUNO: Ayapata, Lechler 2036a (B, E, G, K, LE, P). BOLIVIA: COCHABAMBA: Brooke 6196 (US); Steinbach 9569 (F, GH, K, S-PA, U). LA PAZ: Unduavi, Buchtien 2732 (S-PA, US), 8898 (US).

15. Jamesonia imbricata (Sw.) Hook. & Grev. Icon. Fil. 1: 2. 1831.

Rhizome long creeping, dichotomously branching, ca. 1-5 mm. in diameter with sparse, long roots, the internodes variable in length, the trichomes patent, tan or rigid, appressed and ruddy brown to blackish, 0.5-3.0 mm. long with 1-5 cells near the base, apex acuminate or bulbous. Petiole usually bent and appressed to the rhizome for a short distance before ascending, 1-15 cm. long, 1/20-1/5 as long as the lamina, rarely twice as long, castaneous or atropurpureus, terete or somewhat flattened on the upper surface, ca. 0.5-2.0 mm. in diameter at the apex, stouter or filiform below, glabrous or with sparse trichomes similar to those of the rachis. Lamina once pinnate, ca. 7-80 cm. long, 0.2-1.2 cm. wide, nearly the same size throughout or more slender at the base or apex, ca. 50-400 pinnae, indeterminate or sometimes determinate, the apical bud about the same size or larger than the mature pinnae, with trichomes patent or appressed. Rachis atropurpureus or castaneus, terete or trigonous and the upper surface with an obtuse angle, pubescent, the lower surface usually more densely tomentose, the trichomes as long or slightly longer than the pinnae but not enveloping them, tan or rust colored, the tips clear or darker, the apical cell bulbous or acuminate. Pinnae alternate or subopposite, overlaying the rachis or laterally stacked in 2 ranks, distant, approximate or imbricate, (the basal ones smaller, distant, sterile, sometimes plane, membranous and strongly dentate, persistent or deciduous) orbicular, ovate or long-ovate, truncate and equilateral or inequilateral at the base, patelliform, or the upper surface concave or furrowed, margins enrolled or incurved, 0.75-6.0 mm. long, 1-4 mm. wide, bright or yellowish green, rigid herbaceous; upper surface with few, short, appressed glands or more abundant glands and vernicose, the epidermal cell walls unthickened; lower surface glabrous or tomentose with curled or crispate trichomes, clear, opaque white, tan or rust colored, of 1 or few cells, stalk usually bent or twisted or sometimes nearly straight, 1.0-1.5 mm. long, tan, brown or atropurpureus. Veins slender or moderately broad, in the plane of the upper surface, sunken or raised, dichotomous with acute angles and long branches, or wide angles and moderately long branches, the ends clavate or slightly flabellate, extending to the border. Border broad or narrow, entire, dentate and/or ciliate, membranous, clear, opaque white, tan or rust colored. Sporangia usually abundant near the pinna stalk, fewer on the distal portions of the veins, the stalk short, of 2 tiers, the lower clear or with a cushion of darker cells with intercalary divisions, the annulus with 17-21 indurated cells. Spores tan, light or dark brown, smooth, the equatorial wing narrow or broad and the angles not or scarcely projecting.

The species is principally represented by var. glutinosa which is geographically wide spread and the most distinctive, although polymorphic, member. The two other varieties are associated with it for in each of them there is found two of the critical characters of var. glutinosa — glands on the upper surface of the pinnae and bent pinnae stalks. Variety imbricata combines these characters with some of the features of J. robusta and var. meridensis with some of those of J. canescens. The association of these characters in var. imbricata and var. meridensis and their geographic distributions suggest that they may be of hybrid origin. I have observed var. meridensis in the field and it is sufficiently distinct on several characters of habit to warrant taxonomic recognition. Variety imbricata is insufficiently known and may be reinterpreted as additional, complete material is available; it is, however, a taxon of historical interest in the genus.

KEY TO THE VARIETIES OF JAMESONIA IMBRICATA

- a. Spores tan or light brown; upper surface of the pinnae plane or somewhat concave, the base more or less cordate; veins dichotomous with wide angles, the branches widely diverging and usually short
 - b. Rhizome trichomes amber-colored or light brown, lax, patent; pinnae plane on the upper surface or somewhat concave near the stalk; Colombia, Ecuador, Peru 15A. J. imbricata var. imbricata.
 - b. Rhizome trichomes dark brown or blackish, rigid, appressed; pinnae usually with a central furrow on the upper surface; Venezuela and northern Colombia. 15C. J. imbricata var. meridensis.
- 15A. Jamesonia imbricata var. imbricata Fig. 15A. Map 15A Pteris orbiculata Poir. in Lam. Encycl. 5: 710. 1804, not Houtt. Nat. Hist. 14: 108. 1783. TYPE: J. Jussieu, Pérou (Herb. Jussieu no. 1332) P!, photo GH; isotype: P!, photo, GH.

Pteris imbricata Sw. Syn. Fil. 102. 1806. Based on Pteris orbiculata Poir.

Cheilanthes imbricata (Sw.) Desv. Mém. Soc. Linn., Paris 6: 303. 1827.

Allosorus imbricatus (Sw.) Presl. Tent. 153. 1836.

Pteris imbricata "Cav. Hort. Matrit.", cited by Swartz was not published, see C. Christensen, Dansk Bot. Ark. 93: 7. 1937.

Gymnogramma imbricata (Sw.) Kl. Linnaea 20: 407. 1847.

Jamesonia imbricata (Sw.) Hook. & Grev. var. gracilis Hook. Sp. Fil. 5: 106. 1864. Based on Pteris imbricata Sw.

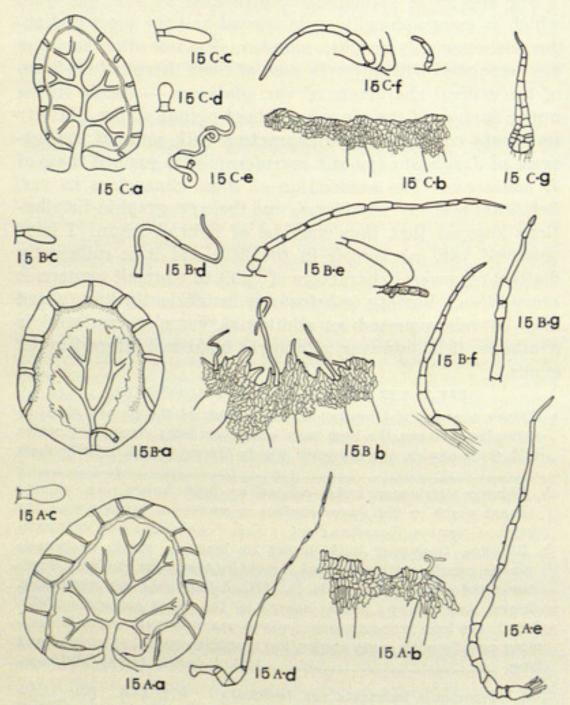


Fig. 15. J. imbricata: 15A. var. imbricata: a, pinna, × 10; b, pinna margin with two vein ends, × 35; c, gland from upper pinna surface, enlarged: d, rachis trichome, × 30; all from J. Jussieu (P); e, rhizome trichome, × 30, from Fosberg 20809 (GH). 15a. var. glutinosa: a, pinna × 10, from Idrobo, et al. 3150 (GH); b, pinna margin with three vein ends, × 35, from Ewan 16364 (GH); c, gland from upper pinna surface, enlarged, from Tryon & Tryon 6085 (GH); d, trichome from lower pinna surface. × 40, from Ewan 16364 (GH); e, rachis trichome, × 30, at right the basal cell and epidermal cells of the rachis enlarged, from Cuatrecasas 7968 (GH); f, rhizome trichome, × 30, from Idrobo et al. 3150 (GH); g, apex of rhizome trichome, × 30, from Tryon & Tryon 6044 (GH). 15c. var. meridensis: a, pinna, × 10; b, pinna margin with two vein ends, × 35; c, gland from upper pinna surface, enlarged: d, gland from lower pinna surface, enlarged; e, trichome from lower pinna surface, × 40; f, rachis trichomes with detail of the basal cell, × 30; g, rhizome trichome, × 30; all from Tryon & Tryon 5801 (GH).

Psilogramme imbricata (Sw.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 334. 1882.

Rhizome trichomes lax, patent, amber-colored or light tan, lighter than the rhizome surface, with usually 1 (-3) cells at the base, the apex acuminate. Lamina indeterminate, the bud of the same size or slightly larger than the mature pinnae, with tan or light brown, patent trichomes. Pinnae orbicular or ovate, the upper surface plane or more or less sunken, slightly inequilateral at the base and somewhat cordate; upper surface glandular, sometimes with a few short trichomes; lower surface tomentose with rust-colored or tan, lax, crispate trichomes, stalk more or less bent. Veins dichotomously branching with wide angles, the branches widely diverging, moderately long. Border rust-colored or tan, entire or dentate and sparsely ciliate. Spores tan or light brown, sometimes shriveled.

The name Jamesonia imbricata has unfortunately been misapplied to specimens of several other species. The de Jussieu collection, at Paris, upon which the name is based. has an unusual combination of characters and there are only a few other collections similar to it. The leaves in the type collection are about the same width throughout with the pinnae imbricate near the apex and distant in the basal portion of the lamina. The pinnae are ovate-cordate or somewhat truncate at the base with a dense tomentum of rust-colored, crispate trichomes on the lower surface and appressed glands on the upper surface. The borders of the pinnae are moderately broad, slightly dentate and sparsely ciliate. There are a few other collections similar to this from Colombia and Ecuador which resemble J. robusta in the light color of the rhizome trichomes, and in the rust colored tomentum on the lower pinna surface. They differ from that species in the shape of the pinnae and in the glands on the upper surface. In these latter characters and also in the bent pinna stalks and somewhat truncate pinna base there is a resemblance to J. imbricata var. glutinosa. On the basis of these characters and the occurrence of each of these taxa in the range of var. imbricata, it is considered a possible hybrid between J. robusta and J. imbricata var. glutinosa.

Colombia, Ecuador, Peru; subparamo, in cutover forest at 3385 m. in Colombia and in dense grass in southern Ecuador at about 3400 m. Additional specimens examined: COLOMBIA. CAUCA: Páramo de Guanacas, Lehmann 4420 (K, US). CUNDINAMARCA: Fosberg 20809 (GH, US). ECUADOR. AZUAY: Páramo de Silván, Barclay & Juajibioy 5399 (GH).

15B. Jamesonia imbricata var. glutinosa (Karst.) comb. nov. Fig. 15B. Map 15B

Jamesonia glutinosa Karst. Fl. Columb. 2: 85, t. 143. 1865. TYPE: H. Karsten, Colombia, monte Guadalupe, Bogotá, 2900 m. LE!, photo GH.

Gymnogramma glutinosa Karst. ex. Mett. Ann. Sci. Nat. V, 2: 209. 1864, nom. nud.

Jamesonia ciliata Karst. Fl. Columb. 2: 85, t. 143, fig. 13. 1865. TYPE: H. Karsten, Venezuela, Mérida LE!, photos GH, W.

Psilogramme glutinosa (Karst.) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 333. 1882.

Gymnogramma ciliata (Karst.) Hieron. Engl. Bot. Jahrb. 34: 477. 1904.

Gymnogramma Mayoris Rosenst. Mém. Soc. Neuchâtel. 5: 55, t. 5. 1912. TYPE: E. Mayor 74, Colombia, Páramo de Cruz Verde, 3500 m. s-PA!, photo BM; isotypes: P! US!.

Jamesonia Mayoris (Rosenst.) C. Chr. Ind. Fil. Suppl. 47. 1913.

Rhizome trichomes patent or slightly appressed, ruddy to dark brown, the same color or more ruddy than the rhizome surface, with 1-3 cells near the base, the apex acuminate or often bulbous. Lamina indeterminate or sometimes determinate, the bud usually smaller than the mature pinnae, with tan or brownish, often bicolorous on the bud, appressed or patent trichomes. Pinnae orbicular, patelliform, with the base equilateral, truncate and incurved adjacent to the stalk; upper surface glandular, usually vernicose; lower surface with opaque white to tan, curled trichomes, sometimes glabrous or nearly so, stalk strongly bent. Veins dichotomously branching usually with acute angles, the branches long and somewhat parallel. Border whitish or tan, entire or dentate and sometimes ciliate. Spores dark brown.

Karsten's epithet was published a year later than that of Mettenius but the latter attributes the species to Karsten without a reference. It seems that Mettenius was aware of Karsten's treatment of this species before it was published in the Flora Columbiae.

Karsten's type of Jamesonia ciliata from Mérida in the herbarium at Leningrad is accompanied by his notes comparing the species with his J. glutinosa and with J. scalaris. The specimen has patelliform pinnae with glands on the upper surface and moderately broad, dentate pinnae borders or narrow ciliate ones. There are other collections similar to this from the Sierra Nevada de Cocuy in Boyacá and from Monserrate, near Bogotá, in Colombia. In J. imbricata var. glutinosa the pinna borders are variable and on the same leaf the basal pinnae may have narrower, more ciliate borders than the younger ones near the apex. Two characters which appear less variable and better characterize the

variety are the strongly bent pinna stalks and the symmetrical pinnae with the bases truncate and incurved near the stalk.

Plants intermediate between var. glutinosa and one of the other species have been most perplexing. Field studies on the populations of these growing on one paramo have been helpful in interpreting the complexity. Where I have found var. glutinosa growing with other species there were usually plants having characters intermediate between the two. On Páramo Palacio and Guasca, north of Bogotá, var. glutinosa occurs with J. rotundifolia and there are many intermediate plants. On Páramo Chisaca, south of Bogotá, var. glutinosa occurs with J. bogotensis and there are some plants appearing intermediate between them. The relationships of var. glutinosa are particularly complicated in regard to the group of J. robusta, J. bogotensis, J. canescens and also with J. rotundifolia. Intermediates with any of these and var. glutinosa may be so modified by the latter that it is not possible to clearly establish which of the former species may be involved.

Variety glutinosa occurs at relatively low altitudes ranging from 2000-3550 m. from Venezuela to southern Ecuador. The lowest record is from Trujillo, Venezuela. Additional specimens examined: VENE-ZUELA. TACHIRA: Páramo de Tamá, Cardona 307 (US, VEN); Steyermark 57403 (US. VEN). TRUJILLO: Funck & Schlim 844 (BM, G, K, LE); Páramo Cristalino, Jahn 139 (US, VEN); Steyermark 55356 (US, VEN). COLOMBIA. Mutis 3084 (US), 3085 (US), 3086 (US), 3098 (US). BOYACA: Barclay & Juajibioy 7555 (GH); Dawe 916 (K); Grubb & Guymer P118 (BM, GH, US). CALDAS: Bro. Tomás 2054 (US). CAUCA: Barclay & Juajibioy 5754 (GH), 5780 (GH); Páramo de Puracé, Cuatrecasas 14610 (GH, US); Grant 10636 (GH, US); Páramo de Gabriel López, Lehmann V. in Nov. 1961 (GH); Pennell 6907 (GH, US); Tryon & Tryon 5991 (COL, GH, S, US), 5993 (COL, GH, NY). CUNDINAMARCA: Guadeloupe, Apollinaire, in 1908 (GH); Cuatrecasas 5414 (GH, US), 7968 (COL, GH, US); Dawe 12 (US); Grant 9413 (US); Haught 5658 (US), 5947 (G, US); Páramo de Chisaca, Jaramillo, in Oct. 1961 (GH); Lindig 118 (GH, K); Monserrate, Little & Little 9446 (COL, US); Perez-Arbelaez 1520 (US); Rusby & Pennell 1264 (GH, US); Páramo de Palacio, Tryon & Tryon 6028 (BM, COL, GH, US), 6033 (GH), 6044 (COL, B, GH, LE, NY, US), Alto de Aguila, 6075 (GH), Cruz Verde, 6085 (COL, F, GH); HUILA-CAUCA: Páramo de Las Papas, Idrobo, et al. 3150 (COL, GH). NORTE DE SANTANDER: Apolinar-Maria 21 (US); Páramo de Tamá, Cuatrecasas et al. 12606 (GH); Páramo de Santurbán, Killip & Smith 19593 (GH, US). PUTUMAYO: Alston 8348 (BM, GH); Páramo de San Antonio del Bordoncillo, Cuatrecasas 11724 (GH, US); Ewan 16364 (GH, US); Schultes & Villarreal 7826 (GH). SANTANDER: Páramo de Santurbán, Barclay & Juajibioy 10433 (GH). VALLE: Cuatrecasas 17839 (GH, US), 20256 (GH, US), 21886 (GH, US). ECUADOR. AZUAY: Páramo del Castillo, Camp 5158 (F, G, GH, K, US).

Specimens examined intermediate between var. glutinosa and Jamesonia rotundifolia: COLOMBIA. CAUCA: Lehmann V. in Nov. 1961 (GH). CUNDINAMARCA: Páramo de Palacio, Cuatrecasas et al. 25642 (US); Fosberg & Villareal 20594 (US); Schultes 18784 (US); Páramo de Palacio, Tryon & Tryon 6035 (GH), 6036 (GH), 6045 (GH), 6049 (COL, GH), 6051 (GH), 6054 (COL, US). SANTANDER: Páramo de las Coloradas, Killip & Smith 18433 (GH, US).

Specimens examined intermediate between var. glutinosa and Jamesonia bogotensis. COLOMBIA. CUNDINAMARCA: Bischler 1515 (COL); Páramo de Chisacá, Cuatrecasas & Jaramillo 25760 (US); Páramo de Chisacá, Tryon & Tryon 6182 (GH, US).

15C. Jamesonia imbricata var. meridensis A. F. Tryon, var. nov. Fig. 15C. Map 15C

Trichomata rhizomatis rigida appressa, obscuro-fuscae vel nigricantia saepe paucis cellulis lata prope basem, pinnae expositae, longiovatae plerumque longiores quam latae, pinnae adaxialiter glandulosae, medio sulcatae, abaxialiter tomentosae trichomatibus crispatis, densis, limbo modice lato, involuto, sporae pallido-fuscae, laeves.

TYPUS: Venezuela, State of Mérida, above Mérida, among rocks near the shore of Laguna de Anteojos, 3900 m. September 16, 1961,

Rolla M. and Alice F. Tryon 5800A (GH).

Rhizome trichomes rigid, appressed, dark brown or blackish, darker than the rhizome surface with 1-5 cells near the base, the apex acuminate. Lamina indeterminate, the bud usually larger than the mature pinnae, with tan or yellow, patent trichomes. Pinnae long-ovate, usually with a central furrow on the upper surface, inequilateral at the base, cordate, the basal lobes sometimes raised above plane of the upper surface; upper surface glandular, sometimes also pubescent; lower surface tomentose with tan to rust colored, crispate trichomes and some capitate glands, stalk slightly bent or nearly straight. Veins dichotomously branching with wide angles, the branches short, widely diverging. Border rust brown, tan or clear, dentate. Spores tan or light amber colored.

At the northern end of the Andes, in Venezuela, around Laguna de Anteojos, and at Aguada above Mérida there are large colonies of these plants growing nearby those of J. canescens. The two are entirely distinct in habit and J. canescens is more abundant over the páramo. Variety meridensis has bright green leaves with large, yellow apical buds and exposed, shining glutinose pinnae. There is a resemblance to var. glutinosa in the somewhat truncate pinna base, bent pinna stalks and glandular indument although the light colored spores and inequilateral form of the pinnae base are similar to J. canescens. There are some specimens

from páramos north in the state of Mérida which resemble var. *meridensis* in having sparsely indumented leaves with small pinnae but these are treated under *J. canescens* since they are not glandular.

Mérida, Venezuela and Magdalena, Colombia, at 4200-4350 m. Additional specimens examined: COLOMBIA. MAGDALENA: Cerro Avión, Cuatrecasas & Castaneda 25149 (US); Romeral-Castañeda 7375 (COL, GH). VENEZUELA. MERIDA: Alston 6851 (BM, GH); Farenholtz 1830 (GH, U); Funck & Schlim 1098 (BM, G, GH, L, LE, P); Gehriger 79a (G, VEN); Moritz 338 (B, BM, K, LE, P, US); Laguna de Anteojos, Tryon & Tryon 5791 (F, GH, NY), 5799 (B, BM, GH), 5810 (GH), 5811 (GH, NY, S), La Aguada, 5801 (GH, S), 5803 (COL, F, GH, P), 5807 (GH); Laguna de Anteojos, Vareschi & K. M. 6862 (VEN), 6863 (VEN).

Jamesonia brasiliensis Christ, Farnkr. Erde 75. 1897. Fig. 16. Map 16

TYPE: Ule, in Mar. 1894, Brazil, Agulhas Negras, Serra de Itatiaia,

2200 m. P!, photos: COL, F, GH, NY, US; isotypes: BM! P!.

Rhizome long creeping, dichotomously branched, slender, ca. 1.0-1.5 mm. in diameter with sparse, roots, the internodes variable in length, the trichomes lax, patent, ruddy brown, about the same color or slightly darker than the rhizome surface, 1.5-2.0 mm. long with 1 or 2 cells near the base, apical cell bulbous. Petiole bent or curled near the rhizome, and appressed for a short distance before ascending 0.5-10.0 cm. long, from 1/12 to 1/3 the length of the lamina, castaneus, terete or plane on the upper surface, slender, ca. 0.5-1.0 mm. in diameter at

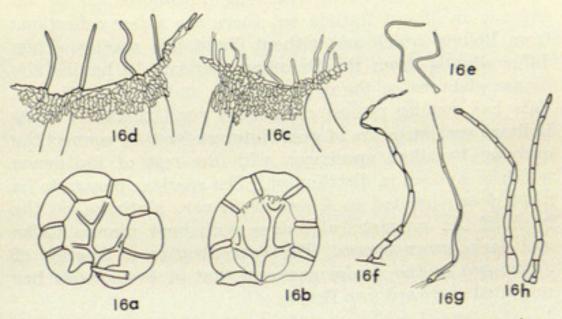
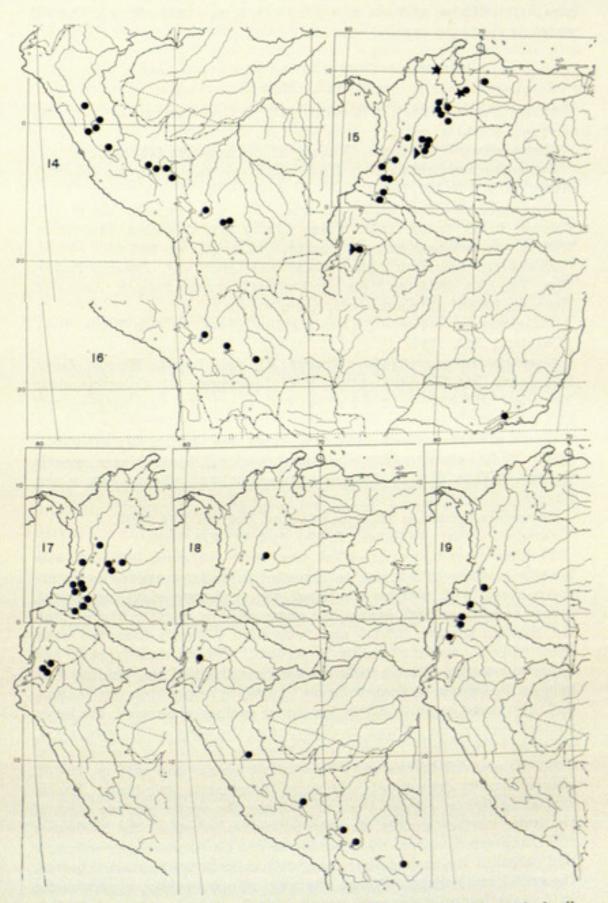


Fig. 16. J. brasiliensis: a, pinna, X 10, from Dusen, in 16/6/1902 (US); b, pinna, X 10; c, pinna margin with two vein ends, X 35; the last two from Tate 327 (US); d. pinna margin with two vein ends, X 35, from Rose & Russell 20505 (US); e, trichomes from lower pinna surface, X 35, from Dusen, in 16/6/1902 (US); f, rachis trichome, X 30, from Rose & Russell 20505 (US); g, petiole trichome, X 30, from Brade 6485 (US); h, rhizome trichomes, X 30, from Rose & Russell 20505 (US).

the apex, glabrous or with sparse, clear trichomes similar to those of the rachis. Lamina once pinnate, ca. 15-40 cm. long, 0.3-0.6 cm. wide, nearly the same size throughout or the base and sometimes the apex slightly narrower, with ca. 175-250 pinnae, indeterminate, the apical bud slightly larger than the mature pinnae, with trichomes patent or slightly appressed. Rachis castaneus, ellipsoidal or trigonous with an obtuse angle on the upper surface, densely pubescent on the lower surface, the trichomes as long or longer than the pinnae, often matted, clear or light tan, concolorous, the apical cell acuminate. Pinnae alternate or subopposite, in 2 ranks overlaying the rachis, imbricate, (the basal ones smaller, distant sterile, persistent) orbicular, sometimes crenate in outline, patelliform, the margin strongly enrolled, equilateral at the base, 2.0-3.5 mm. long, 2.0-3.5 mm. wide, bright green, herbaceous; upper surface sparsely pubescent with long, clear trichomes or glabrous, the epidermal cell walls unthickened; lower surface with moderately dense tomentum of clear, curled, one or few celled trichomes, stalk bent, ca. 0.25-0.50 mm. long atropurpureus. Veins slender, in the plane of the upper surface or slightly raised, dichotomous with wide angles, the branches long or moderately long, the ends clavate or acute, extending to the border. Border usually moderately broad, sometimes extended at the vein ends, entire or slightly undulate, ciliate, membranous, clear or opaque white. Sporangia few, on veins mostly adjacent to the pinna stalk, not on the distal portion, the stalk short, of 2 tiers with intercalary cell divisions, the lower tier may be brown and with 1 or few trichomes, the annulus of 12-18 indurated cells. Spores dark brown, smooth, the equatorial wing moderately broad, the 3 angles not or scarcely projecting.

Jamesonia brasiliensis was long considered to be an endemic on Mount Itatiaia but there are a few collections from Bolivia which are without doubt this species. They differ slightly from the Brazilian material in having the pinnae glabrous on the upper surface and the collection of Tate has smaller pinnae of a more rigid texture. These Bolivian specimens are of great interest for they connect the outlying Brazilian specimens with the rest of the genus which is Andean in distribution. The species appears to be most closely related to J. imbricata var. glutinosa on the basis of the symmetrical pinnae with bent pinnae stalks and dark brown spores. The concentration of species of Jamesonia in the Andes suggests that J. brasiliensis has migrated eastward into Brazil.

Northern to central Bolivia and Mount Itatiaia, Brazil, at 2200-2600 m. Additional specimens examined: BOLIVIA. COCHABAMBA: Comarapa, Herzog 1944 (B, S, US); Steinbach 9596 (US). LA PAZ: Cocopunco, Tate 327 (US). BRAZIL. RIO DE JANEIRO: Serra de Itatiaia, Brade 6485 (B, S-PA, US); Dusén 400 (B, BM, GH, K, LE, P, S,



MAPS 14-19. Map 14, J. scalaris. Map 15, J. imbricata, the triangles at the localities of var. imbricata, the dots at the localities of var. glutinosa, the stars at the localities of var. meridensis. Map 16, J. brasiliensis. Map 17, J. verticalis. Map 18, J. blepharum. Map 19, J. cinnamomea.

S-PA, US); Glaziou 5327 (B, K, P), 7016 (B, K, P, S, US); Rose & Russell 20505 (US), 20514 (US).

Jamesonia verticalis Kunze, Bot. Zeit. 2: 739. 1844. Fig. 17. Map 17

TYPE: Hartweg 1504, Colombia BM!, photos: COL, F, GH, NY, US; isotypes: B! GL! K! P!.

Gymnogramma verticalis (Kunze) Kl. Linnaea 20: 410. 1847.

Jamesonia imbricata (Sw.) Hook. and Grev. var. verticalis (Kunze) Hook. Sp. Fil. 5: 107. 1864.

Gymnogramma verticalis (Kunze) Kl. var. humilis Karst. Fl. Columb. 2: 86, t. 143. 1865. TYPE: Lindig 311, Colombia, Manzanos, 2800 m. B!; isotypes: BM! K! (photos: COL, F, GH, NY, US) P!.

Jamesonia imbricata (Sw.) Hook. and Grev. var. Pearcei Baker, Syn. Fil. 514. 1874, as "var. J. Pearcei". TYPE: Pearce, Andes of Ecuador, 10,000' K!, photos: COL, F, GH, NY, US.

Psilogramme verticalis (Kunze) Kuhn, Fests. 50 Jub. Reals. Berl. (Chaetop.) 382, 1882.

Gymnogramma verticalis (Kunze) Kl. var. frigida Hieron, Engl. Bot. Jahrb. 34: 475. 1904. TYPE: F. C. Lehmann 5002, Colombia, near Popayan, 2800-3200 m. B!; photos: COL, F, GH, NY, US; isotypes BM! GH! K! P! US!.

Gymnogramma tolimensis Hieron. Engl. Bot. Jahrb. 34: 475. 1904. TYPE: F. C. Lehmann 2401, Colombia, montis Alto de Oteras, montis Tolima, 3200 m. Jan. 11, 1883 B; isotypes: K! LE!, photos: COL, F, GH, NY, US.

Jamesonia tolimensis (Hieron.) C. Chr. Ind. Fil. 374, 1905. Jamesonia Pearcei (Baker) C. Chr. Ind. Fil. 374, 1905.

Rhizome creeping or somewhat erect near the apex, dichotomously branched, stout ca. 3-5 mm. in diameter with dense roots, the internodes short, with petioles congested, the trichomes rigid, appressed, lustrous ruddy or dark brown, the same color or slightly darker than the rhizome surface, 2.0-2.5 mm. long with 1-4 cells near the base, apex bulbous, exuding, rarely acuminate. Petiole usually bent and appressed to the rhizome before ascending, 2.5-45.0 cm. long, 1/4 as long as the lamina or frequently up to 4 times longer than the lamina, dull, glutinous, atropurpureus, the upper surface channeled, the lower surface convex, ca. 1-3 mm. in diameter at the apex with dense, rigid, appressed trichomes. Lamina pinnatisect or pinnate at the base, ca. 8-40 cm. long, 0.7-4.5 cm. wide, broadest above the base with ca. 50-160 pinnae, usually determinate, the apex pinnatisect, acuminate. Rachis similar or lighter colored than the petiole, the upper surface sulcate, the lower surface convex, densely pubescent, crustose, the trichomes rigid, appressed, or somewhat patent, tan or bicolorous short or longer and tufted at the base of the pinna, with cells at the base dark brown, the apical cell bulbous. Pinnae alternate or subopposite, approximate, in 2 ranks laterally disposed, usually adnate, (the basal ones smaller, distant, fertile, persistent) long-ovate to oblong, rarely orbicular, the base broad to narrowly attached along the central channel of the rachis or the acroscopic side partly free and imbricate, usually auriculate or lobed, sometimes entire, plane or slightly patelliform, 0.8-2.2 cm. long, 0.2-1.0 cm. wide, yellow-green, sometimes brownish along the veins adjacent to the rachis, coriaceous; upper surface vernicose with appressed glands, the epidermal cell walls slightly thickened; lower surface with rigid, erect, capitate, clear, tan or light brown, short trichomes of one or few cells, especially abundant along the veins. Veins broad, in the plane of the upper surface or usually raised, dichotomous with acute angles, the branches long, nearly parallel, the vein ends broad, clavate to flabellate extending nearly to the margin. Border usually undifferentiated or narrow, sometimes protruding at the veins, fimbriate with cilia similar to the trichomes of the lower pinna surface. Sporangia abundant along the veins especially adjacent to the rachis in the central portion of the pinnae, fewer on the distal portion of the veins, the stalk short, of 2 tiers the lower one usually brownish, several cells broad sometimes with 1 or more trichomes, the annulus of 17-19 indurated cells. Spores dark brown, smooth to slightly verrucose especially on the distal face, the equatorial wing moderately broad, the 3 angles not or slightly projecting.

There is remarkable plasticity in the form of the leaves in *J. verticalis* especially in the length of the petiole, the size of the pinnae and the elaboration of the margin. In one collection the length and breadth of the leaves vary considerably and on a single leaf there is a broad range in pinna size. There are some collections from Cauca and Cundinamarca, Colombia with mostly small, entire pinnae with strongly enrolled margins which have been distinguished as var. *frigida* and var. *humilis*. They are not recognized here because of the variability in these characters and the occurrence of intermediate specimens.

Jamesonia verticalis differs from other species in Jamesonia in the elongate pinnae which are mostly adnate but the relationship appears to be closest to J. cinnamomea. A collection of Fosberg 20954, from Páramo de Sumapaz, in Meta, south of Bogotá is included in J. verticalis on the adnate pinnae and short stalks of the sporangia but it resembles J. cinnamomea in the orbicular pinnae form.

Jamesonia verticalis is regarded as the least specialized member of a group including J. cinnamomea and J. ble-pharum. The adnate pinnae in J. verticalis, however, appear to be a character that is more specialized than in the other two. This group represents an independent line in Jamesonia, originating from a species similar to Gymnogramma Mathewsii. There are similarities between this species and J. verticalis in the form of the pinnae, the channeled petioles,

the short, rigid trichomes on the lower surface of the pinnae and the rectangular form of the epidermal cells.

Jamesonia verticalis has a broader geographic and altitudinal range than J. cinnamomea, occurring in all three of the Cordilleras of Colombia and in southern Ecuador, at 1800-3500 m. Additional specimens examined: COLOMBIA. Santa Ana, Langlassé 99 (B, G, GH, K, P, US). ANTIOQUIA: Cerro de la Vieja, Bro. Daniel 1729 (US); Páramo de Sonsón, Ewan 15708 (GH, US); Kalbreyer 1325 (B, K). CALDAS: Cerro Tatama, Pennell 10471 (GH, US). CAUCA: Alto del Duende, Cuatrecasas 18859 (GH, US); Hartweg 1048 (K); Lehmann 1268 (K, L, US), 4428 (B, K, P, US), 5705 (B, K, P, US); Mount El Derrumbo, Pennell 7492 (GH, s, US); Páramo de Buena Vista, Pittier 1149 (US); El Tambo, von Sneidern 1127 (B, S, US). CUNDINAMARCA: Grant 10201 (US); St. John 20526 (GH, US). HUILA: Cuatrecasas 8793 (COL, US); Juzepczuk 6602 (LE); Stübel 182 (B, US), 298 (B). META: Páramo de Sumapaz, Fosberg 20954 (US). PUTUMAYO: Alston 8402 (BM, GH); Fosberg 20344 (US); Alta de Cruz, Foster & Foster 2053 (COL). VALLE: Cuatrecasas 18023 (GH, US). ECUADOR. André 4534 (F, GH, K, US). AZUAY: Páramo del Castillo, Camp E4815 (F, GH, US), 4884 (U, US); Crespi 52 (US).

18. Jamesonia blepharum A. F. Tryon, sp. nov. Fig. 18. Map. 18
Trichomata rhizomatis rigida, appressa, pallida usque obscurofusca vel atropurpurea, laminae saepe determinatae vel gemmae
quam pinnae minores, glutinosae trichomatibus appressis, rachis aliquid sulcata vel adaxialiter infrequens plana, pinnae adnatae vel
subsessiles, orbiculares, patelliformes, rigide herbaceae, pinna adaxialiter vernicosa trichomatibus glutinosis, abaxialiter trichomatibus
capitatis, glandulosis, nervis copiosis, nervis gracilibus, dichotomis
angulis acutis, ramis longis aliquanto parallelibus, sporae obscurofuscae, raro pallidae, laeves vel papillatae.

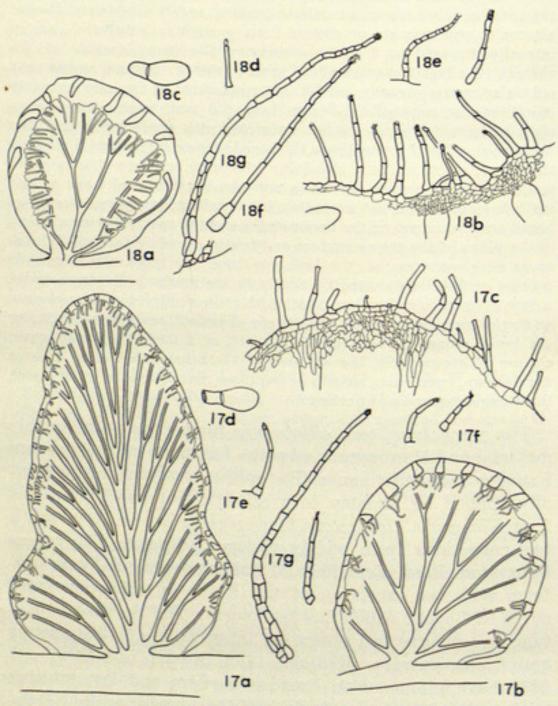
TYPUS: Peru, Pampayacu, Jan. 16, 1927, Ryozo Kanehira 148, GH; isotypus: US.

Rhizome long creeping, dichotomously branched, ca. 1.0-2.5 mm. in diameter with sparse, long roots, the internodes variable in length, with petioles sometimes congested, the trichomes rigid, appressed, lustrous light to dark brown or atropurpureus, usually darker than the rhizome surface, ca. 1.0-1.5 mm. long with usually 1 or 2 cells near the base, apical cell acuminate or bulbous and exuding. Petiole often bent and appressed to the rhizome before ascending, 3.5-22.0 cm. long, from 1/6 to nearly 1/2 as long as the lamina, usually dull blackish, sometimes lighter, nearly castaneus, terete or channeled on the upper surface, ca. 1.0 mm. in diameter or slightly less at the apex, usually with appressed, glutinous trichomes. Lamina once pinnate, ca. 10-55 cm. long, 0.5-1.0 cm. wide, with 60-220 pinnae, the lamina nearly the same size throughout or the base and apex more slender, sometimes determinate, the apical bud usually smaller than the mature pinnae, with appressed or patent, glandular trichomes. Rachis similar in color or lighter than the petiole, shallowly sulcate, rarely plane on the upper surface, usually crustose or vernicose and with appressed,

rarely patent trichomes especially on the lower surface, longer and tufted at the base of the pinnae, often with basal cells lighter colored. the apex usually bulbous, sometimes exuding, rarely acuminate. Pinnae alternate, approximate or distant, rarely slightly imbricate, usually laterally disposed in 2 ranks overlaying the upper surface of the rachis, (the basal ones smaller, usually sterile, distant, persistent) orbicular, entire, usually patelliform, equilateral at the base or nearly so, adnate or subsessile, 1-8 mm. long, 1-6 mm, wide, yellow-green, rigid herbaceous; upper surface vernicose with appressed glands, the epidermal cell walls sometimes thickened; lower surface with clear or tan, short, erect, capitate, glandular trichomes, or longer trichomes of several cells, longer on the veins, sometimes curled and more or less matted, stalk oblique not exceeding 1.0 mm. long, atropurpureus often broad and decurrent on the upper surface of the rachis. Veins slender, in the plane of the upper surface or slightly raised or sunken, dichotomous with acute angles, the branches long, nearly parallel, the ends clavate or flabellate extending nearly to the margin. Border narrow, a row of cells broader than long, with cilia similar to the trichomes on the lower pinna surface. Sporangia abundant, sometimes obscuring the lower pinna surface, the stalk short, of 2 tiers, the lower one a cluster of brown cells, the annulus of 17-19 indurated cells. Spores dark brown, rarely tan, smooth or papillose, the equatorial wing broad, the 3 angles scarcely projecting.

The name Jamesonia ciliata was formerly applied to this material and Hieronymus cites the Lehmann collection from Ecuador under that name. The epithet was, however, originally applied by Karsten to a collection of another species from Venezuela. Jamesonia blepharum is known from only a few collections from widely disjunct stations. The collections from Peru, Ecuador and Colombia are relatively uniform with the exception of the Philipson collection from north of Bogotá which has tan spores. The Bolivian collections are diverse and somewhat intermediate to this species and J. cinnamomea. Williams 1152, in part, and Steinbach 8370 have pinnae with broader borders and lax, whitish trichomes on the lower surface of the pinnae; while Cárdenas 1024 has unusually long, lax leaves with dense, white, crispate trichomes on the lower pinna surface. These collections resemble J. cinnamomea in having relatively long stalked pinnae but I am placing them in J. blepharum, with some reservation, on the relatively smaller pinnae, the short stalked sporangia and dark, appressed rhizome trichomes.

Jamesonia blepharum is most closely related to J. cinnamomea in several characters and intermediate to this and J. verticalis.



Figs. 17 AND 18. Fig. 17. J. verticalis: a, pinna, X 5, from Cuatrecasas 18859 (GH); b, pinna, X 5, from St. John 20526 (GH); c, pinna margin with two vein ends, X 35, from Fosberg 20344 (US); d, gland from upper pinna surface, enlarged, from Cuatrecasas 8793 (US); e, capitate trichome from lower pinna surface, enlarged, from Cuatrecasas 18023 (GH); f, petiole trichomes, the apical cells with exudate, X 30, from Pittier 1149 (US). Fig. 18. J. blepharum: a, pinna, X 10; b, pinna margin with three vein ends, X 35; c, gland from upper pinna surface, enlarged; d, glandular trichome from lower pinna surface, enlarged; e, rachis trichomes, the right with exudate at the apex, X 30; f, rhizome trichome with exudate at apex, X 30; all from Kanehira 148 (GH); g, rhizome trichomes showing the basal cells, X 30, from Philipson et al. 2443 (COL).

At disjunct stations from central Bolivia to northern Colombia, from 1500-3400 m. Additional specimens examined: COLOMBIA. CUNDIN-AMARCA: Páramo de la Calera, Philipson et al. 2443 (BM, COL). ECUADOR. Loja: Lehmann 5707 (K, P, US). PERU. CUZCO: Bües 1824 (US), 1908 (US), 1914 (US). BOLIVIA. LA PAZ: Cárdenas 1024 (GH); Tolapampa, Williams 1152 (US). SANTA CRUZ: Comarapa, Steinbach 8370 (GH, K, S).

Jamesonia cinnamomea Kunze, Bot. Zeit. 2: 738. 1844. Fig. 19. Map 19

TYPE: Hartweg 1516 BM!, photos: COL, F, GH, NY, US; isotypes B! BM! G! GH! K! LE! US!.

Gymnogramma cinnamomea (Kunze) Kl. Linnaea 20: 407. 1847.

Jamesonia imbricata (Sw.) Hook. and Grev. var. cinnamomea (Kunze) Hook. Sp. Fil. 5: 107. 1864.

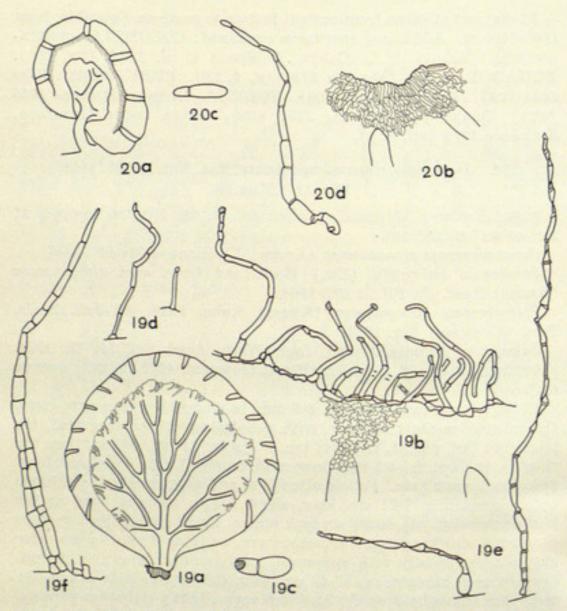
Psilogramme cinnamomea (Kunze) Kuhn, Fests. 50 Jub. Reals.

Berl. (Chaetop.) 334, 1882.

Jamesonia brunnea Maxon, Jour. Wash. Acad. Sci. 14: 72. 1924.

TYPE: L. Mille 42, Ecuador, Mount Guamani, 4000 m. US!; isotype
GH!.

Rhizome creeping, stout, ca. 2-5 mm. in diameter with sparse roots, the internodes short or long, with petioles sometimes congested, the trichomes lax, patent, lustrous tan or golden brown, lighter than the rhizome surface, 1.5-2.5 mm. long with usually 1 (-3) cells near base, apical cell acuminate. Petiole often bent and appressed to the rhizome before ascending, 7-21 cm. long, about 1/5 to twice as long as the lamina, usually dull, ruddy or dark brown, terete or the upper surface channeled and the lower surface convex, ca. 2 or 3 mm. in diameter at the apex, usually with appressed, ruddy or dark brown trichomes. Lamina once pinnate, ca. 38-43 cm. long, 0.8-1.5 cm. wide nearly the same size throughout or the base and apex slightly narrower with ca. 70-170 pinnae, sometimes determinate, the apical bud usually large, up to 4 times larger than the mature pinnae, with a tomentum of partly appressed, cinnamomeus trichomes. Rachis similar in color to the petiole, the upper surface sulcate or with 2 shallow lateral grooves, densely pubescent especially on the lower surface, with crisped, patent or r'gid, appressed trichomes which are longer and tufted at the base of the pinnae, with the basal cells sometimes lighter colored, the apex usually bulbous. Pinnae alternate, imbricate, often approximate, in 1 or 2 closely placed rows over the rachis, (the basal ones smaller, sometimes distant, sterile, persistent) orbicular, entire, patelliform, the margin enrolled, equilateral at the base, 2-10 mm. long, 2-9 mm. wide, yellow-green, coriaceous; upper surface with appressed, glutinous trichomes, often vernicose, the epidermal cell walls slightly thickened; lower surface with clear or tan, short, erect, capitate trichomes of 1 or few cells and with longer tan to brown, curled trichomes, of several cells, near the stalk of the pinna, stalk oblique, usually short, rarely up to 2 mm. long, castaneus or atropurpureus often broad and slightly decurrent on the upper surface of the rachis. Veins broad, in the plane of the upper surface, often slightly raised,



Figs. 19 and 20. Fig. 19. J. cinnamomea: a, pinna, × 5; b, pinna margin with two vein ends, × 35; c, gland from upper pinna surface, enlarged; d, capitate trichomes from lower pinna surface, × 30; e, rachis trichomes, × 30; f, rhizome trichomes showing the basal cells, × 30; all from Cuatrecasas 14713 (GH). Fig. 20. J. ceracea: a, pinna, × 10; b, pinna margin with two vein ends, × 35; c, gland from upper pinna surface, enlarged; d, rachis trichome, × 30; all from Pennell 2607 (GH).

dichotomous with moderately wide angles, the branches long and nearly parallel, the ends clavate or acute, ending short of the border. Border narrow, rarely broader, with a row of cells broader than long with trichomes having the apical cell bulbous and sometimes glandular. Sporangia abundant, the stalk usually as long or longer than the capsule, with intercalary cell divisions and sometimes with trichomes, the annulus of 18-21 indurated cells. Spores dark brown, smooth, the equatorial wing broad, the 3 angles prominently projecting.

This is a most distinctive species easily recognized by the long, robust leaves with numerous, orbicular pinnae and the usually large, ruddy brown leaf bud. In a few collections the apex may be completely unrolled. Most specimens are rela-

tively uniform but a collection from Ecuador, Espinosa 956, has unusual dark brown, rigid, appressed rhizome trichomes and some lobed pinnae.

The species is most closely related to Jamesonia blepharum and J. verticalis on several characters and appears to be more specialized than these in the broader pinnae margins, elongated sporangia stalks and large leaf buds. However, the lax, light colored rhizome indument and the stalked pinnae appear less specialized.

Jamesonia cinnamomea occurs from central Ecuador to southern Colombia, at 3100-5000 m. The highest altitude at which the genus is reported is a collection of this species from Mount Chimborazo, Ecuador. Additional specimens examined: COLOMBIA. CAUCA: Volcán de Puracé, Cuatrecasas 14713 (GH, US); Pérez Arbeláez & Cuatrecasas 5930 (COL, US); von Sneidern 1685 (G, S). NARINO: Volcán de El Galeras, Ewan 16321 (GH, US); Volcán de Pasto, Jameson 12 (B, E, G, GL, K, LE, US). ECUADOR. André 3262 (GH, K, US); Espinosa 956 (GH); Sodiro 28 (GH, P, S-PA, U). CHIMBORAZO: Mount Chimborazo, Asplund 7821 (GH, S); Heinrichs 946 (F, G); Hitchcock 21971 (GH, US); Rimbach 35 (GH, US), 72 (GH, US), 132 (US), 312 (B, S-PA), 538 (S-PA). IMBABURA: Volcán de Cayambe, Drew E439 (US); Monte Cayambe, Jameson 503 (G, GH); Little & Paredes C. 6895 (US). TUNGURAHUA: Mount Caribuayrazo, Asplund 8480 (GH, S).

DUBIOUS AND EXCLUDED NAMES

Jamesonia adnata Kunze, Farrnkr. 2: 80, t. 133, f. 1. 1851. TYPE: Linden 1006, Colombia B. = Polypodium moniliforme Lagasca.

Jamesonia ceracea Maxon, Jour. Wash. Acad. Sci. 14: 73. 1924. Fig. 20. TYPE: F. W. Pennell 2607, Colombia, Mt. Chuscal, west of Zipaquirá Us!; isotype: GH!. The collection consists of several detached, sterile leaves with small pinnae having very broad, indusioid borders and copious, ceraceous indument on the lower surface. In these characters the material is so distinctive from other species in the genus it is understandable that it was described as new. It is in fact so unique that I regard it as aberrant. There are a few collections of Jamesonia imbricata var. glutinosa with ceraceous indument on the upper surface of the pinnae but this Pennell collection is the only material that I have seen in which such indument is found on the lower pinna surface. I suspect that it is a hybrid of one of the complexes involving var. glutinosa.

Jamesonia crespiana Bosco, Nuovo Giern. Bot. Ital. n. s. 45: 147, t. 10. 1938. TYPE: C. Crespi, Ecuador, Gualaceo — Culebrilla, 2500 m. Herb. Miss. Salesiane. This is not a Jamesonia since it is described as having broad, ovate rhizome scales and from the photograph it appears

to be a species of Polystichum.

Jamesonia elongata (Hook. & Grev.) J. Smith, Hist. Fil. 168. 1875 = Eriosorus elongatus (Hook. & Grev.) Copel.

Jamesonia grisea Maxon ex Pittier, Man. Pl. Usual. Venez. 193. Caracas. 1926, nom. nud.

Jamesonia hispidula Kunze, Bot. Zeit. 2: 739. 1844. TYPE: Moritz 72, Caracas, Venezuela. This collection was not found at either B or BM. It is out of the geographic range of Jamesonia and is perhaps an Eriosorus.

Jamesonia imbricata var. culebriliensis Bosco, Nuovo Giorn. Bot. Ital. n. s. 45: 147. 1938. TYPE: C. Crespi, Ecuador, Gualaco et Cuebrilla, 2500 m. Herb. Miss. Salesiane. From the description of the alate rachis and dentate segments this cannot be a Jamesonia but I cannot place it in any genus with certainty.

Jamesonia paleacea Kunze, Bot. Zeit. 2: 739. 1844. TYPE: Linden 505, Caracas, Venezuela BM!; isotype: BR, photo, GH! = Polystichum pycnolepis (Kunze) Mett.

LITERATURE CITED

- Bower, F. O. 1928. The Ferns. Vol. 3. The Leptosporangiate Ferns. University Press. Cambridge, England.
- Brade, A. C. 1942. A composição da flora Pteridófita do Itatiaia. Rodriguésia 6: 26-43.
- CHRISTENSEN, C. 1938. Filicinae, in Manual of Pteridology. Martinus Nijhoff, The Hague.
- COPELAND, E. B. 1947. Genera Filicum. Chronica Botanica. Waltham, Massachusetts.
- Cuatrecasas, J. 1934. Observaciones Geobotánicas en Colombia. Trab. Mus. Nac. Cien. Nat. Madrid Ser. Bot. 27: 1-144.
- ERDTMAN, G. 1957. Pellen and Spore Morphology/Plant Taxonomy.

 Almqvist and Wiksells. Stockholm.
- Fosberg, F. R. 1944. El Páramo de Sumapaz. Jour. N. Y. Bot. Gard. 45: 226-234.
- dense and B. multifidum. Amer. Fern Journ. 51: 175-179.
- HOLTTUM, R. E. 1946. A Revised Classification of Leptosporangiate Ferns. Jour. Linn. Soc. Lond. Bot. 54: 123-158.
- Jameson, W. 1865. Synopsis Plantarum Aequatoriensium. Quito, Ecuador.
- KRAMER, K. U. 1957. A revision of the genus Lindsaea in the New World with notes on allied genera. Acta Bot. Neerl. 6: 97-290.
- Manton, I. 1958 Chromosomes and Fern phylogeny with special reference to "Pteridaceae." Jour. Linn. Soc. Lond. Bot. 56: 73-92.
- SIMPSON, G. G. 1961. Principles of Animal Taxonomy. Columbia University Press. New York.
- SMITH, A C. AND I. M. JOHNSTON. 1945. A phytogeographic sketch of Latin America, in Plants and Plant Science in Latin America. Chronica Botanica. Waltham, Massachusetts.
- SMITH, L. B. 1962. Origins of the flora of southern Brazil. Contrib. U. S. Nat. Herb. 35: 215-249.
- THOMPSON, J. M. 1918. The anatomy and affinity of certain rare and primitive ferns. Trans. Roy. Soc. Edin. 52: 363-397.
- TRYON, A. F. AND D. M. BRITTON. 1958. Cytotaxonomic studies of the fern genus Pellaea. Evolution 12: 137-145.

- TRYON, R. M. 1944. Dynamic phytogeography of Doryopteris. Amer. Jour. Bot. 31: 470-473.
- WILSON, K. A. 1959. Sporangia of the fern genera allied with Polypodium and Vittaria. Contrib. Gray Herb. no. 185: 97-127.



Tryon, Alice F. 1962. "A monograph of the fern genus Jamesonia." *Contributions from the Gray Herbarium of Harvard University* (191), 109–197. https://doi.org/10.5962/p.336405.

View This Item Online: https://www.biodiversitylibrary.org/item/122620

DOI: https://doi.org/10.5962/p.336405

Permalink: https://www.biodiversitylibrary.org/partpdf/336405

Holding Institution

Missouri Botanical Garden, Peter H. Raven Library

Sponsored by

Missouri Botanical Garden

Copyright & Reuse

Copyright Status: Permission to digitize granted by rights holder

Rights Holder: Harvard University Herbaria

License: http://creativecommons.org/licenses/by-nc-sa/3.0/
Rights: https://www.biodiversitylibrary.org/permissions

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.