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THE EVOLUTION AND SYSTEMATICS OF LEAVENWORTHIA (CRUCIFERAE)[1]

REED C. ROLLINS

Different kinds of higher plants differ markedly in their sensitiveness to the various features of their environment, as do organisms in general. Some species, for example, exist in a wide variety of fluctuating sites, characterized by diverse conditions, without any obvious difficulty or radical responsive reaction. Others, at the opposite extreme, are very sensitive to every facet of their environment and exist only under a strictly limited pattern of conditions. Undoubtedly, nearly all imaginable combinations of intermediates occur as well. For certain types of evolutionary studies, plants closely restricted (and therefore adapted) to a relatively uniform set of environmental conditions are highly desirable. This is particularly true where several different evolutionary units have developed but all have retained their adaptation to the same set of edaphic conditions. Such a situation permits an examination of evolutionary patterns and trends under circumstances where the effects of certain aspects of the environment are minimal and the selective effects of other aspects are more clearly defined and readily seen. We have been fortunate in selecting a genus with many desirable attributes for detailed evolutionary and systematic studies and the present paper undertakes to set forth our findings.

Leavenworthia was initially selected for detailed study because of certain obvious contrasts with *Lesquerella*, another genus of the *Cruciferae*, which has a number of species growing in the same general area. The most important of

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these contrasts was that the four species of *Leavenworthia* of central Tennessee (cf. Map 2) are sympatric in their occurrence, often being present in exactly the same habitat, whereas the species of *Lesquerella* of the same area are allopatric in their distribution (Rollins, 1955). A second important contrast was that the Central Basin species of *Lesquerella* hybridized readily (Rollins, 1957) while those of *Leavenworthia* showed no evidence of natural hybridization even though the plants of several species grew in close proximity to each other. It was assumed and subsequently shown experimentally that well established genetic barriers exist between the Tennessee species of *Leavenworthia.* The auriculate species of *Lesquerella* of Tennessee have a uniform chromosome number, n = 8. At the outset of this study, on the other hand, two chromosome numbers were known in *Leavenworthia,* n = 11 and n = 15.

One of our major objectives has been to see, if possible, what the conditions and circumstances were that brought about speciation in these two genera of the same family, in the same area but with such different genetic, cytological and geographical characteristics. Furthermore, we were interested in speciation within *Leavenworthia* itself. It was hoped that some insight into the conditions favoring speciation would be gained and that the pattern of evolution within the genus could be satisfactorily elucidated.

From the work of Baldwin (1945) it was known that plants of *Leavenworthia stylosa* are self-incompatible and that this contrasts with the situation of self-compatibility found in plants of *L. exigua, L. torulosa* and *L. uniflora.* Our desire to exploit this fact to determine whether self-incompatibility is positively correlated with a higher intrapopulation variability than is found in populations where self-compatibility prevails has not been fully realized. However, we discovered populations characterized by self-compatibility in otherwise self-incompatible species together with a neat correlation of anther position and pollen discharge. These facts are brought out below.

General Observations

Leavenworthia is a small distinctive genus of the Cruciferae which has an unusually close adaptation to cedar glades exhibiting certain physical characteristics. The most important of these characteristics appears to be a combination of shallow soil depth and dolomitic limestone thinly bedded in such a way as to maintain a temporary high moisture content at or very near the surface. Often the limestone is horizontally bedded and is covered with but a few inches of soil or it may be completely barren of soil in some spots. Such situations are extremely wet during late winter and early spring and become very dry during the summer months. Thus, a set of extremes of moisture stress is presented to the plants growing there. The severity of these conditions is brought out by Freeman (1933). These areas vary as to size and may be as small as a few square meters or as large as a square kilometer or more. Quarterman (1950) characterizes such areas in Tennessee as open glades. The high moisture required by *Leavenworthia* is provided at some sites by slightly tilted limestone strata that bring water to the surface. This type of habitat is common in the ozark region of Missouri and is found at the one location where *Leavenworthia* occurs in Texas, at San Augustine. An excellent description, including photographs, of some dolomitic glades of east-central Missouri is given by Erickson, Brenner and Wraight (1942). It is clear that the glades of all areas where *Leavenworthia* grows are not completely comparable, particularly as to slope and relief. Those of Tenneessee, Alabama and Oklahoma occupy relatively flat areas, while many of the others are on slopes of varying degrees of steepness. Most of the *Leavenworthia* glades appear to be on dolomitic limestone of Ordovician age. Harper (1926, p. 49) suggests that there are no true cedar glades in northern Alabama but he may not have considered the principal *Leavenworthia* areas since he specifically mentioned only the Coosa Valley.

It should be emphasized that high soil moisture content in late winter and early spring appears to be an important feature of suitable sites for the abundant occurrence of *Leavenworthia*. There are many places in Alabama, Tennessee, Kentucky and Missouri where all other conditions, except that of soil moisture, appear to be met but the plants do not occur at these sites. Every species of the genus (with slight deviations in *L. uniflora*) seems to require approximately the same set of conditions, whether it be in Kentucky, Tennessee, Alabama, southeastern Oklahoma or eastern Texas. This leads to the view that certain of the physiological requirements are genus-wide and therefore must have been rather solidly fixed into its genetic make-up early in its evolutionary development. This close adaptation to a rather narrow and rigid set of edaphic conditions appears to have been an important factor influencing the direction and extent of evolution within the genus.

All species of *Leavenworthia* bloom early in the spring. Known flowering dates range from late February into May. The time of flowering varies from year to year, depending upon temperature, moisture and the severity of winter freezing. The plants are classed as winter annuals. Seed germination takes place from September onward and the individual plants persist through the winter months as rosettes of radical leaves.

The most recent study of *Leavenworthia*, that of Baldwin (1945), was primarily cytogeographic. In it, he concluded that the genus consisted of four well defined species. Since then, I have shown (1956) that *L. aurea* is confined to restricted areas in southeastern Oklahoma and extreme eastern Texas, and that the plants of Tennessee previously called *L. aurea* really represent a fifth species, *L. exigua*. As shown below, there are two additional species, *L. crassa* and *L. alabamica* and several varieties heretofore unrecognized. As known at present, the genus consists of eleven taxa. A taxonomic treatment of the genus is given below.

GENERIC RELATIONSHIPS

The direct relationships of *Leavenworthia* to other genera of the *Cruciferae* are not established. From such treatments of the family as those of von Hayek (1911) and Schulz (1936), where *Leavenworthia* and *Cardamine* are placed next to or close to each other in the tribe *Arabideae*, it is usually inferred that these two genera are closely related. The same conclusion might be drawn from the fact that Michaux (1803) described the first known species of *Leavenworthia* in the genus *Cardamine*. However, I cannot see any real evidence from the morphology of *Leavenworthia* to suggest a closer link to *Cardamine* than to several other possible genera. The fruits of *Cardamine* are singularly different from those of *Leavenworthia* and the seeds of the latter are unlike any found in *Cardamine*. The straight or nearly straight embryo of *Leavenworthia* is unusual in the *Cruciferae*. *Leavenworthia* does not tie in directly with *Cardamine*, or any other American genus of the *Cruciferae*, for that matter, in a way that would provide significant information about the origin of any of the present day species. Because of the lack of closely related genera, the present study has dealt only with the species of *Leavenworthia* and only in a casual way with intergeneric considerations. Perhaps the suggestion of Torrey (1837, p. 94) that "upon the whole I consider it more nearly related to *Selenia* than to any other known genus" is still pertinent.

MATERIALS AND METHODS

The present study of *Leavenworthia* was begun in 1955. At that time, we started collecting herbarium specimens and taking notes on populations in the field. Additional collections, including cytological fixations for chromosome number determination, were made in the spring of 1956. The following year, both flowering and fruiting materials were collected, together with packets of seeds. Intensive work on the genus, involving greenhouse and garden cultures, was started in the winter of 1959. Several approaches have been focused toward providing a maximum understanding of the genus. These included detailed studies of wild populations; random seed sampling of these same populations to produce cultures of plants in the greenhouse and experimental garden, where careful comparative measurements were made; making numerous interspecific pollinations together with an analysis of the fertility of resulting hybrids through pollen analysis and/or progeny testing; and study of herbarium specimens to provide a historical and geographical basis to the overall findings.

In establishing living cultures, seeds were germinated in petri dishes and the young seedlings transferred to three-inch clay pots or to planting bands in flats. In the greenhouse, the plants were brought to maturity in three-or-four-inch pots. The planting bands were used to transfer young plants to the experimental garden. In general, growth was satisfactory, although not outstanding, in Cambridge soils. Vermiculite, leaf-mold or peat moss was added to soil to make up the greenhouse mixture.

Self-compatibility tests were made by hand selfing on both isolated and bagged plants. Seed-set or lack of it was used as the criterion as to whether the plants were self-compatible or not.

Field sampling was done in an arbitrary manner. The same procedure was followed in taking the flowers and fruits that provided the measurement data of both Tables 3 and 4. This consisted of walking in a straight direction across a population. At each step, a single fully opened flower was picked from the plant nearest the toe of the foot. Similarly, in taking fruits, a mature, fully filled, green fruit, just approaching the onset of ripening, was picked. The flowers were fixed immediately in FAA for later measurement with the use of a binocular dissecting scope. The fruits were measured as soon as they were accumulated, before any appreciable wilting had begun. Under these circumstances, the fruits were turgid and it was efficient to use a thickness gauge for width, thickness and style length measurements. The silique length measurement was taken with a millimeter rule.

In sizing up a population for sampling, the most important consideration was always the appropriateness of the maturity stage of the material to be gathered. The next step was to determine the approximate extent of more or less contiguous plants and to visually mark the area into a circle. Each sampling originated at a different point on the circumference of the circle and extended to an opposite point on the same circumference. Sometimes several such marches, always originating at a different point, were required to produce the total sample for a given population. By following this procedure, a particular area of a given population was sampled only once.

CYTOLOGY

Baldwin's (l. c.) extensive reports of chromosome numbers of four species of *Leavenworthia* have been confirmed by our findings. As shown in Table I, where only new counts are reported, *L. uniflora, L. torulosa* and *L. stylosa* have 15

TABLE 1. CHROMOSOME COUNTS OF LEAVENWORTHIA[2]

SPECIES	LOCATION	COLLECTOR & NUMBER	*n*
L. alabamica			
var. **alabamica**			
	ALABAMA. — Franklin Co.:		
	9 mi. e. Russellville	Rollins 55186[2]	11
	7 mi. e. Russellville	Rollins & Chambers 57135	11
	Lawrence Co.:		
	6 mi. w. Moulton	Rollins & Channell 5631	11
	3 mi. s. Hatton	Rollins & Channell 5642	11
	4 mi. w. Moulton	Rollins & Chambers 5712	11
	½ mi. e. Landersville	Rollins & Chambers 5713	11
	3 mi. s. w. Moulton	Rollins 5929	11
var. **brachystyla**			
	ALABAMA. — Morgan Co.:		
	3 mi. w. Falkville	Rollins 5926	11
	5 mi. w. Falkville	Rollins 5932	11
L. aurea			
	OKLAHOMA. — Choctow Co.:		
	6 mi. w. Ft. Towson	Rollins 5582	24
	1 mi. w. Ft. Towson	Rollins & Chambers 5774	24
	McCurtain Co.:		
	4.7 mi. n. Idabel	Rollins & Chambers 5766	24
	7.3 mi. n. w. Idabel	Rollins & Chambers 5771	24 [22]
L. crassa			
var. **crassa**			
	ALABAMA. — Morgan Co.:		
	¼ mi. n. Danville	Rollins & Chambers 5721	11
	¼ mi. n. Danville	Rollins & Chambers 57141	11
	2 mi. e. McKendry	Rollins 5925	11
	2.5 mi. w. Danville	Rollins 5931	11
	5 mi. w. Falkville	Rollins et al 6015	11
	Near Harrin Creek	Rollins 6122b	11
	Lawrence Co.:		
	8 mi. e. Wren	Rollins & Chambers 57139	11
var. **elongata**			
	ALABAMA. — Morgan Co.:		
	6 mi. sw. Falkville	Rollins et al. 6021	11
L. exigua			
var. **exigua**			
	TENNESSEE. — Marshall Co.:		
	1 mi. n. Chapel Hill	Rollins & Chambers 5731	11
	2 mi. s. Chapel Hill	Rollins & Chambers 57143	11
	Wilson Co.:		
	3 mi. s. Gladeville	Rollins & Chambers 57149	11
	GEORGIA. — Catoosa Co.:		
	1 mi. e. Ft. Oglethorpe	Rollins & Chambers 5704	11

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[2] Voucher specimens with corresponding collector and collector's number are deposited in the Gray Herbarium.

Table 1. *(Continued)*

SPECIES	LOCATION	COLLECTOR & NUMBER	*n*
	Walker Co.:		
	7 mi. s. Ft. Oglethorpe	Rollins & Chambers 5705	11
var. **lutea**			
	ALABAMA. — Jefferson Co.:		
	1 mi. n. e. McCalla	Rollins & Channell 5643	11
var. **laciniata**			
	KENTUCKY. — Bullit Co.:		
	6 mi. e. of Sheperdsville	Rollins 6201	11
L. stylosa			
	TENNESSEE. — Davidson Co.:		
	2 mi. n. e. Lavergne	Rollins 55161	15
	Rutherford Co.:		
	Near Lavergne	Rollins & Channell 5615	15
	6 mi. n. Walter Hill	Rollins & Channell 5611	15
	13 mi. s. e. Murfreesboro	Rollins & Channell 5651	15
	4 mi. e. Lascassas	Rollins 5902	15
	Wilson Co.:		
	3 mi. n. Lebanon	Rollins & Channell 5610	15
	3 mi. s. e. Lebanon	Rollins 5910	15
	5 mi. e. Lebanon	Rollins et al. 6001	15
L. torulosa			
	KENTUCKY. — Warren Co.:		
	12 mi. n. U. S. 68 on State Rt. 1083	Rollins & Channell 5906	15
	TENNESSEE. — Bradley Co.:		
	1.5 mi. e. Cleveland	Rollins 5901	15
	Davidson Co.:		
	14 mi. s. e. Nashville	Rollins & Channell 5620	15
	Giles Co.:		
	3.5 mi. s. w. Pulaski	Rollins & Chambers 5723	15
	Marshall Co.:		
	7 mi. n. Lewisburg	Rollins & Channell 5625	15
	4 mi. s. w. Cornersville	Rollins & Channell 5626	15
	1 mi. n. Chapel Hill	Rollins & Chambers 5732	15
	2 mi. s. Chapel Hill	Rollins & Chambers 57142	15
	Rutherford Co.:		
	3 mi. s. Lavergne	Rollins & Channell 5616	15
	1 mi. n. Lavergne	Rollins & Chambers 57145	15
	Wilson Co.:		
	12 mi. w. Lebanon	Rollins & Channell 5908	15
	Watertown	Rollins & Channell 5911	15
	2 mi. s. Norene	Rollins & Channell 5912	15
L. uniflora			
	TENNESSEE. — Bedford Co.:		
	6 mi. s. Eagleville	Rollins & Channell 5660	15
	Marshall Co.:		
	1.5 mi. s. Lewisburg	Rollins & Chambers 5726	15

Table 1. *(Continued)*

SPECIES	LOCATION	COLLECTOR & NUMBER	n
	Rutherford Co.:		
	5 mi. s. Murfreesboro	Rollins 55298	15
	13 mi. e. Murfreesboro	Rollins & Channell 5651	15

pairs of chromosomes. The counts for *L. exigua* are n = 11. This is the same as Baldwin's number for the plants of this species although the number was reported by him under the name of *L. aurea.* Both *Leavenworthia crassa* and *L. alabamica* have 11 pairs of chromosomes. Baldwin did not investigate material of either of these species nor did he have true *Leavenworthia aurea*, which usually has 24 pairs of chromosomes.

The chromosomes of *Leavenworthia* are relatively small and difficult to handle, particularly where the number is rather high, as in *L. aurea.* No less than forty-seven different plants, representing several independent accessions, were studied critically in determining the chromosome number of the latter species. We are convinced that n = 24 is the usual number in this species but the possibility that some plants have n = 23 or n = 22 could not be wholly ruled out.

A very different picture of chromosome number relationships in *Leavenworthia* from that given by Baldwin (l. c.) emerges from our studies. His assumption that the three species *(L. stylosa, L. torulosa, L. uniflora)*, with 15 pairs of chromosomes, are hexaploids must be seriously questioned in view of the fact that three other species *(L. alabamica, L. crassa, L. exigua)* have 11 pairs. Actually, the presence of n = 11, n = 15 and n = 24 in different species of a genus as small and closely knit morphologically and physiologically as *Leavenworthia* is difficult to explain on the basis of ordinary polyploid relationships. In my estimation, it is not profitable to speculate as to the fundamental number in this genus or to guess as to what possible ploidy level we may be dealing with in any given species. The facts are that excellent pairing of chromosomes is regularly found in *L. alabamica, L. crassa* and *L. exigua*, the three species with n = 11. A similar statement cannot be made concerning the three n = 15 species, or *L. aurea*, n = 24. Rather frequent irregularities were found in *L. stylosa* and were particularly prevalent in *L. aurea* where "multivalent tendencies" were repeatedly seen in late prophase stages of meiosis. However, these irregularities were probably of a transient nature because the expected effects of the observed irregularities, such as a reduction in the quality of pollen, did not show up in any of the species. All seven species behave reproductively as diploids. On other grounds as well as chromosome number, it is suggested that *L. aurea* is a polyploid. This much seems certain.

As mentioned above, the chromosomes of *Leavenworthia* are small. We could not work with the morphology satisfactorily but two sizes of chromosomes are evident in the meiotic preparations of certain species. This is particularly noticeable in *L. stylosa* (as was also indicated by Baldwin l. c.) where three of the fifteen chromosomes are considerably smaller than the other twelve. One of the three small chromosomes is somewhat smaller than the other two. Similarly, *L. torulosa* has three chromosomes smaller than the other twelve, with one of the three smaller than the other two. In *L. alabamica*, one of the eleven chromosomes is smaller than the other ten and in *L. exigua* there is one smaller chromosome as compared to the other ten of its chromosome complement. Preparations of other species did not show similar size differences. However, it should be clearly stated that this aspect of the study was tangential to the main emphasis and was not pursued intensively for its own sake.

Some items of evidence from cytology bear directly on considerations of the direction in which the chromosome number shift may have taken place in the genus. These are the small chromosomes, more numerous in the $n = 15$ species than in the $n = 11$ species, the more frequent irregularities, including "stickiness," in the $n = 15$ species as compared to the $n = 11$ species, and the suggestion of eleven homologous chromosomes between the eleven-paired *L. exigua* and the fifteen-paired *L. stylosa* (see below under interspecific hybridization). We interpret these as minor indications that the chromosome number shift may have been in the direction of the higher number. One thing seems unequivocal, the shift from $n = 11$ to $n = 15$, or the reverse if that were the case, was successful only once during the evolutionary development of the genus. However, there is no conclusive evidence to support the idea that the direction of evolution has been from the *L. crassa* — *L. alabamica* complex toward the higher chromosome numbered species. It is quite possible that the presently known chromosome numbers are not the same as those of the progenitors of the modern species. If this latter is the case, then we must assume that extinction of species played a role in permitting the emergence of the rather unusual chromosome number relationships now to be found in the genus.

As suggested above, the high chromosome number of $n = 24$ found in *L. aurea* suggests a polyploid origin for that species. In view of the close morphological resemblance between *L. exigua* var. *lutea* and *L. aurea*, it is not unlikely that var. *lutea* or a similar plant figured in the origin of *L. aurea* in some manner. There is no evidence that var. *lutea* itself produced *L. aurea* by chromosome doubling and the addition of extra chromosomes and this is not suggested but it may be involved as one of the taxa in such a process. Grant (1956) has made the point that polyploidy in annuals or short-lived perennials is frequently associated with autogamy, particularly where hybridization occurs. Autogamy is present in both var. *lutea* and *L. aurea*.

INTERSPECIFIC HYBRIDIZATION

In marked contrast to the situation in the auriculate-leaved species of *Lesquerella* of the same area (Rollins, 1957), the species of *Leavenworthia* of the Central Basin of Tennessee do not hybridize. The four species, *L. exigua*, *L. stylosa*, *L. torulosa* and *L. uniflora*, occur on the same site in numerous places (cf. Map 2), often within inches of each other. I have repeatedly examined the plants of all four species where they are intimately intermingled and in no instance have I been able to detect evidences of interspecific hybridization. Results of attempted crossings between these four species were similarly negative, with one exception, as shown in Fig. 1. The broken lines of this crossing polygon indicate that no hybrids were formed from reciprocal pollinations of *L. stylosa*, *L. torulosa* and *L. uniflora*. However, when pollen of *L. exigua* was carried to the flower stigmas of *L. stylosa*, some hybrids resulted. These hybrid plants, though vegetatively vigorous, were

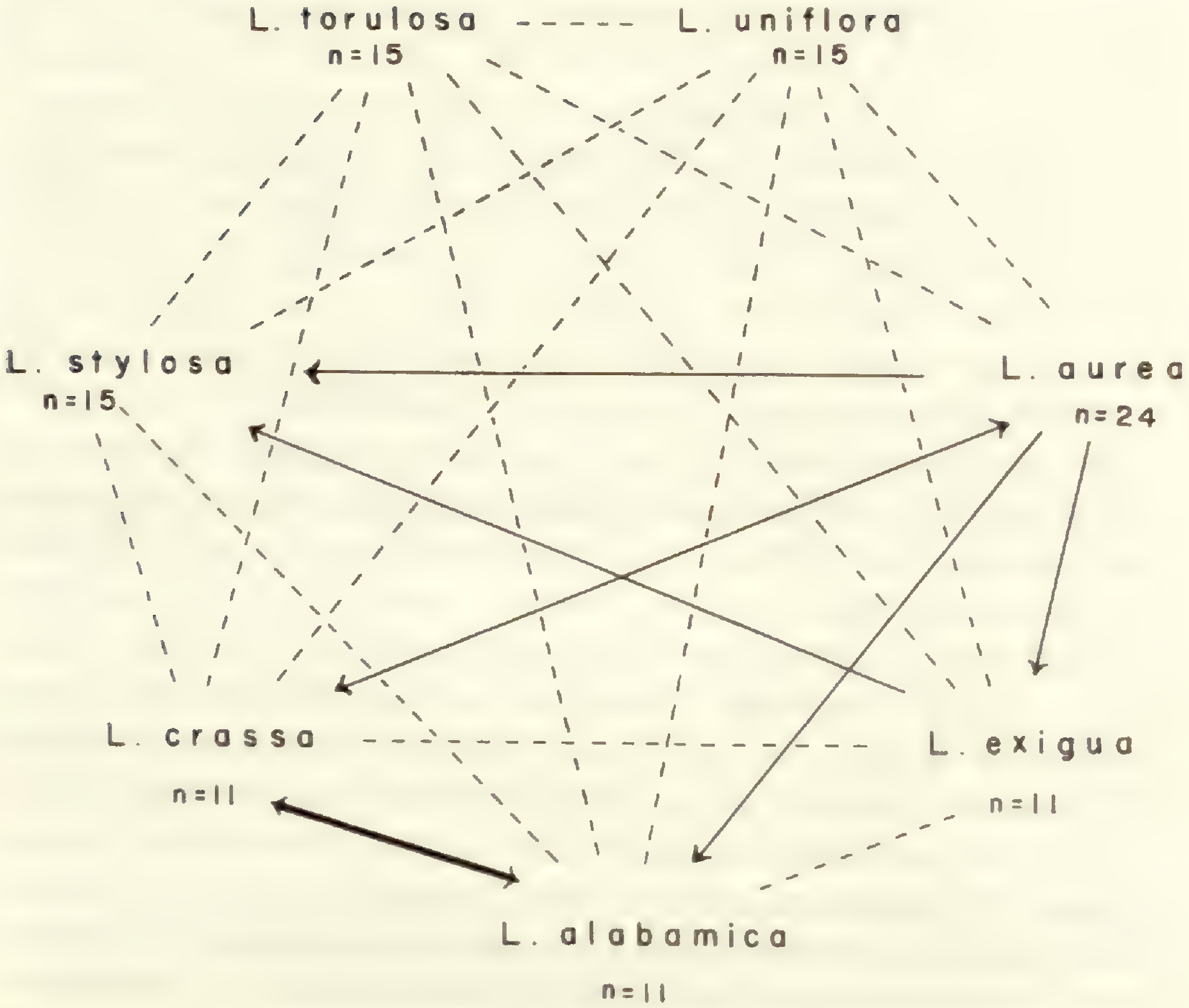

FIG. 1. Diagram showing attempted crosses between the species of *Leavenworthia*. All crosses were attempted reciprocally. Numerous pollinations using several to many cultures of each species were made. Attempted crosses where no progeny resulted are indicated with a broken line. Thin solid lines indicate F_1 hybrids were produced but these proved to be sterile. The thick solid line indicates fertile F_1 hybrids were produced. The point of an arrowhead indicates the direction in which pollination was successful in producing F_1 progenies.

found to be pollen sterile and would not produce viable seeds in attempted back crosses to the parental species. In other crosses, *L. crassa* × *L. aurea*; *L. stylosa* × *L. aurea*; *L. alabamica* × *L. aurea*; and *L. exigua* × *L. aurea*, vegetatively vigorous hybrids were produced but, in each case they were pollen sterile and both intercrossing within hybrid families and back crossing to the parental species were unsuccessful. With the exceptions of the *L. crassa* × *L. aurea* and *L. exigua* × *L. stylosa* crosses, it should be noted that in all the rest, hybrids were produced only when pollen of the polyploid *L. aurea* was carried to the other species. The unidirectional success with polyploid pollen is not unexpected in view of the frequency of similar results in other plants.

A cytological analysis of various crosses involving *L.*

aurea revealed marked signs of hybridity and sterility. In crosses of *L. alabamica* and *L. aurea*, there was considerable fluctuation in the amount and degree of irregularity from one preparation to the next. Although pairing was irregular and the number of pairs was difficult to determine because of the small size of the chromosomes, the number of pairs centered around a mode of eleven. Univalents were always conspicuous and their number fluctuated from 5 to more than 11. These sometimes occurred within the area of the metaphase plate but frequently they were well outside of it. There was evidence of multivalent associations of the chromosomes but these could not be interpreted with certainty as to whether they were trivalents, tetravalents, etc. Both tetrads and pollen were found to be irregular. On the basis of 500 observations of the appropriate stage of *L. alabamica* × *L. aurea* F_1 hybrids, the following results were obtained: monads .8 to 1.6%; diads 0-6%; triads 1.2 to 2.4% and tetrads 85 to 90%.

Similar overall cytological results were obtained from an analysis of F_1 hybrids between *L. crassa* and *L. aurea*. The only additional observation was that a more marked asymmetrical distribution of the chromosomes appeared to take place. However, it is probable that this does not signify a real difference between the patterns of irregularity of the two interspecific crosses. In both crosses the tendency to form about eleven bivalents suggests a loose homology between the genomes of *L. alabamica* and *L. crassa* on the one hand and a portion of the genome of *L. aurea* on the other.

No definite cytologically readable figures could be found in hybrids of two different crosses between *L. aurea* and *L. stylosa*. In a few instances univalents were seen but in most fixations the pollen mother cells were shrunken and devoid of contents. In many flowers, the anthers were not fully developed and in some instances the anthers were completely abortive. In the crosses between *L. aurea* and *L. exigua*, appropriate stages of meiosis rarely occurred. Meiotic irregularity was evident in the one collection that yielded good stages where univalents, bivalents and multivalents were observed.

The cytological picture in F_1 hybrids of crosses between *L. exigua* and *L. stylosa* is one of irregularity. Univalents and multivalents are nearly always present. Three, four or sometimes more univalents are usual. An inversion bridge with fragment was seen quite often. In one p. m c., eleven bivalents and four univalents were seen. This provides the thinnest of evidence that eleven of the fifteen chromosomes of *L. stylosa* have remote homologues in *L. exigua.*

The F_1 hybrids of crosses between *L. crassa* and *L. alabamica* are cytologically in complete contrast with the other interspecific hybrids. The meiotic process is not wholly devoid of irregularities, but these are rather minimal and seem to pertain to timing rather than to chromosome incompatibility. Eleven bivalents are regularly formed and although some "stickiness" and "lagging" occasionally occur, these features are relatively infrequent.

From all points of view, the one successful interspecific cross was that of *L. alabamica* × *L. crassa.* In this case, fertile F_1 hybrids were produced reciprocally in several combinations involving collections from different localities. Furthermore, subsequent generations produced good pollen and viable seed. *L. alabamica* and *L. crassa* are strikingly different, particularly with respect to the morphology of their fruits. These differences, as brought out below where the species are considered from the taxonomic point of view, characterize the species throughout their geographic ranges and the only "break-down" of these distinctive features is in a few small zones where *L. crassa* var. *crassa* and *L. alabamica* var. *brachystyla* are in contact, and several other areas where *L. crassa* var. *elongata* and *L. alabamica* var. *brachystyla* come together in cultivated fields. Under present conditions, where cultivated fields and pastures have largely replaced the cedar glades, resulting in the destruction of the original vegetation, natural interspecific hybridization is actively taking place and hybrid swarms are to be found here and there in the area, ranging from a few miles south to a few miles east of McKendry, Morgan County, Alabama.

In addition to the experimental production of hybrids, in June 1959 four plants of *L. crassa* var. *crassa* and four plants of *L. alabamica* var. *alabamica* were placed interspaced in a single row in my home garden in Wellesley, Massachusetts, completely isolated from all other *Leavenworthia* plants. Lively insect visitation among the eight plants was observed during the flowering period. The seeds from these eight plants were sown at random in an area 1 × 2 meters in size. The seeds were permitted to germinate naturally, which occurred during September and October, 1959. From that time until the present, March 1963, the same plot has been devoted to the natural growth of *Leavenworthia*. Numerous vigorous plants have resulted from the seed shed naturally each year. Other than weeding and occasional watering, no special care has been given to the "volunteer" plants that have come up each fall. These "rosette" plants have over-wintered very well and have produced vigorously flowering plants each spring.

The first progeny of the initial eight plants consisted of a mixture of F_1 hybrids and the parental species *L. crassa* and *L. alabamica*. The numbers of plants of each species exceeded those of the interspecific hybrids in this generation. However, in each succeeding generation, the relative proportion of hybrids has increased. After the collection and analysis of additional data from this "natural" experiment, the information will be separately presented. Three facts of interest are: (1) interspecific hybridization between *L. crassa* and *L. alabamica* under quasi-natural conditions produces a hybrid swarm; (2) some species of *Leavenworthia* are capable of surviving at least for several years without any substantial protection or care, far outside of their natural geographical range; (3) these particular species and their hybrid progenies are very poor competitors with other plants. The latter point was suspected for *Leavenworthia* from field observations. In the plot described above, it was tested by leaving one corner unweeded during the spring of 1962. The principal weed was *Poa annua*. Well established plants of *Leavenworthia* were killed out completely by *Poa* in the entire area where it was permitted to grow unchecked. Over thirty *Leavenworthia* plants died in less than two months in the area invaded by *Poa annua*, while over three hundred plants grew normally in the rest of the plot.

THE BREEDING AND REPRODUCTIVE SYSTEMS

Self-incompatibility predominates in *L. stylosa*, *L. crassa* and *L. alabamica*. The other species are self-compatible and vary somewhat as to the amount of autogamy that takes place. All of the populations of *L. stylosa* tested were self-incompatible and this result agrees with the work of Baldwin (l. c.). *L. crassa* var. *crassa* and *L. alabamica* var. *alabamica* are also largely self-incompatible insofar as they have been investigated by me. However, there is an indication from the work of David Lloyd that some populations of *L. alabamica* var. *alabamica* are at least partially self-compatible. Of considerable significance is the fact that the tested populations of both *L. crassa* var. *elongata* and *L. alabamica* var. *brachystyla* are highly self-compatible. From having worked with growing material produced from seeds of a number of wild populations, we have no reason to doubt that self-compatibility largely characterizes these two varieties. The shift from self-incompatibility to self-compatibility, accompanying the evolution of distinct varieties in both species, is significant in itself but it is particularly so when considered together with the fact that such a shift is a general feature of the genus. The switch in breeding system has occurred in the 15-paired chromosome group and in the 11-paired group. Within the 11-paired chromosome group of species, it has taken place within two distinct species and there is a strong probability that it occurred independently of these in the line leading to *L. exigua* and *L. aurea*. If the development of self-compatibility in the species *L. crassa* and *L. alabamica* took place relatively more recently than in the two main evolutionary lines of the genus, as we have good reason to believe, then self-compatibility came about independently four different times. Leaving out all supposition, the evidence is incontrovertable that self-compatibility arose independently at least three times. This event probably took place many more than four times during the course of the evolution of the genus to its present state.

In his survey of self-incompatibility in the *Cruciferae*, Bateman (1955) was impressed by the fact that both self-incompatibility and self-compatibility occur in most tribes of the family and in nearly all genera in which as many as four species had been tested. He does not cite any instance where both systems occur naturally within the same species, as is the case in *L. alabamica* and *L. crassa*. There is no reason known to me why the compatibility system should not differ within species as well as between species of the same genus, the latter being a well known situation in the *Cruciferae*. Since this is an evolutionary step that is frequently taken, it is perhaps surprising that it has not been previously emphasized as an intraspecific phenomenon.

The question of direction of shift of the compatibility type, from self-incompatibility or the reverse, is a pertinent one. There is no intrinsic reason why the shift should not go from self-compatibility to self-incompatibility and this probably occurs, if only rarely. However, the ease with which the shift might occur in one direction or the other is wholly different. Most of the available data concerning the *Cruciferae* indicate that a relatively complex multi-allelic genetic system is involved in producing self-incompatibility. This requires the development of a genetic system that actually prevents delivery of the pollen content (i. e. the male gametes) to the female gametophyte. In a sporophytic system, such as that widely found in the *Cruciferae*, incompatible pollen is inhibited before pollen tube penetration of the stigma. The release of such a polygenic system providing positive prevention of autogamy might require only a single mutation. Thus, while the development of a complex of interacting genes could evolve only gradually and probably over a fairly long time span, perhaps with several steps before it resulted in obligate self-incompatibility, the shift from self-incompatibility to self-compatibility could be relatively easy and require only a short period. The widespread presence of self-incompatibility in the family argues for its early evolutionary development, perhaps even its presence as a characteristic of the progenitors of the family. On these grounds, added to those relating to the particular nature of the species themselves, we believe self-incompatibility preceded self-compatibility both within and between species of *Leavenworthia*.

Anther position. — One of the very interesting findings in the present study has been that a general correlation exists between an extrorse position of the anthers of the two sets of paired stamens and self-incompatibility of the particular taxon on the one hand and a partially introrse or introrse position and self-compatibility on the other. Against these changes of position of the paired stamens, the single short stamens in the *Leavenworthia* flower maintain their anthers in the introrse position. In the self-incompatible populations of *L. alabamica, L. crassa* and *L. stylosa,* the anthers of the paired stamens are essentially extrorse and the pollen is delivered away from the stigmatic surface. A contrastingly different pattern is characteristic of the self-compatible species where the anthers of the paired stamens are either partially or wholly introrse. Here, the pollen is delivered toward the stigmatic surface, enabling a high degree of autogamy to occur. In Plate 1, two views of the upper part of the paired stamens, together with the stigma and a small portion of the style of ten different taxa, are shown. Examples of an extrorse position are seen in Plate 1, fig. 1a and 1b of *L. stylosa,* and in fig. 9a and 9b of *L. alabamica* as well as in other figures of the plate where the extrorse position is less definite. Examples of introrse anthers are fig. 2a and 2b of *L. aurea* and 8a and 8b of *L. uniflora* in the same plate. The anther positions of both paired and single stamens and their position in relation to the stigma are illustrated in Plates 2 and 3.

An analysis of the anther position in a number of wild populations and growing cultures show that a range from extrorse to introrse occurs in the genus. Five diagrammatic patterns, as indicated in Fig. 2, have been developed to represent the principal pattern types seen in the living material. Table 2 gives a record of the stamen pattern and the compatibility type in a number of populations and cultures. These data indicate a strong tendency for the anther pattern to shift from extrorse to introrse concomitantly with a shift from self-incompatibility to self-compatibility. These correlated changes have occurred during speciation in the genus and apparently are continuing to occur as a part of the evolutionary process during the present period. This is shown by the fact that there are self-compatible populations within species that are otherwise mostly self-incompatible. Such is the case in both *L. alabamica* and *L. crassa.* In Table 2, it may be seen that stamen patterns A and B tend to characterize the self-incompatible *L. alabamica* var. *alabamica* and *L. crassa* var. *crassa* but that patterns C and D are characteristic of the self-compatible *L. alabamica* var.

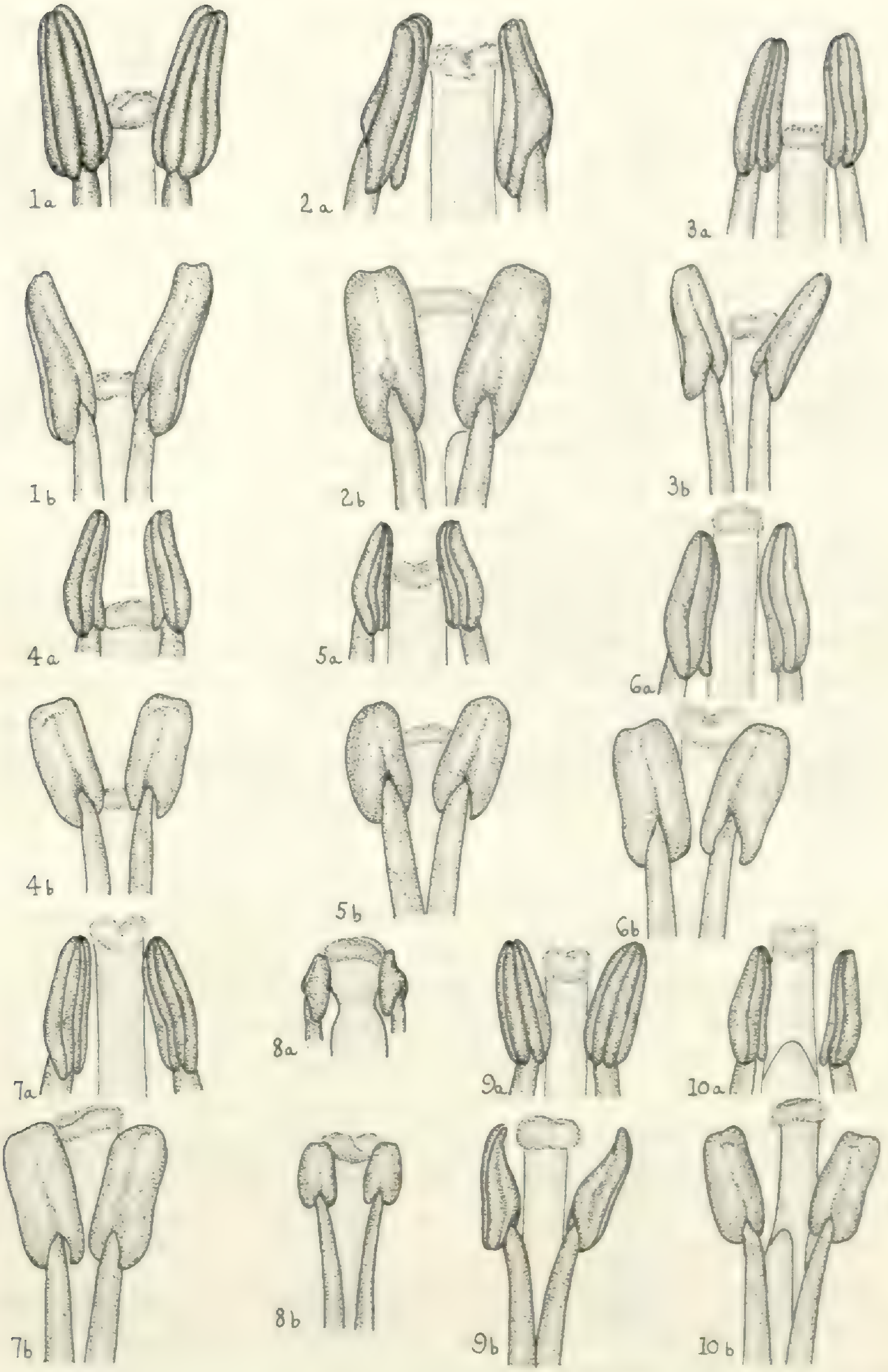

PLATE 1. Anthers in relation to stigma. The figures designated "*a*" in each case show one anther from each of the two stamen pairs. The lines of dehiscence of the anthers are to be seen in most of these. The figures designated "*b*" show the anthers of a single pair. Fig. 1a, b, *L. stylosa;* Fig. 2a, b, *L. aurea;* Fig. 3a, b, *L. crassa* var. *crassa;* Fig. 4a, b, *L. alabamica* var. *brachystyla;* Fig. 5a, b, *L. exigua;* Fig. 6a, b, *L. crassa* var. *elongata;* Fig. 7a, b, *L. torulosa;* Fig. 8a, b, *L. uniflora;* Fig. 9a, b, *L. alabamica;* Fig. 10a, b, *L. exigua* var. *lutea.* All figures × 10. Drawings by Ruth Hsu Chen.

brachystyla and *L. crassa* var. *elongata.* It should be noted that some variability is present in each population. Patterns C, D and E are found in the self-compatible species.

The differences in anther orientation apparently are due to rotations of the filaments at the point of insertion on the receptacle of the flower. There is no evidence of twisting of the filaments or of a change in orientation of the anther with respect to the filament.

Flower Size. — Early in the present study it was observed that there are substantial differences in the flower size of different species of *Leavenworthia.* In some instances, these differences are of considerable magnitude, as between *L. uniflora* and *L. stylosa.* In comparing other species, for example *L. crassa, L. alabamica* and *L. stylosa,* the flowers proved to be similar in size. The significance of these differences became evident when a correlation between large flowers and self-incompatibility was realized. Since the self-incompatible species are obligate outcrossers, they are wholly dependent upon insect pollination for survival and large flowers are a distinct advantage. Whenever a population becomes self-compatible, insect attraction is no longer vital and the maintenance of large flowers is not especially favored by selection. Table 3 presents measurement data for petal length, petal width and sepal length for a number of populations of nine taxa. The site where each population grew or was grown is given because the flower size is somewhat influenced by conditions during growth. This may be seen by a comparison of measurements on the same accession, No. 57142, grown both in the greenhouse and in the experimental garden. However, such differences due to the influence of local factors of the environment do not transcend the larger differences in flower size distinguishing some of the species.

The range in flower size in *Leavenworthia* is graphically shown in Fig. 3, in which the mean petal length and width of selected populations are represented by ideographs and the mean sepal length by an adjacent vertical bar. Fig. 3 was prepared from data in Table 3. It is quickly evident from visual comparisons within Fig. 3 that the largely self-incompatible *L. alabamica, L. crassa* and *L. stylosa* are large-flowered as compared to the self-compatible *L. aurea,*

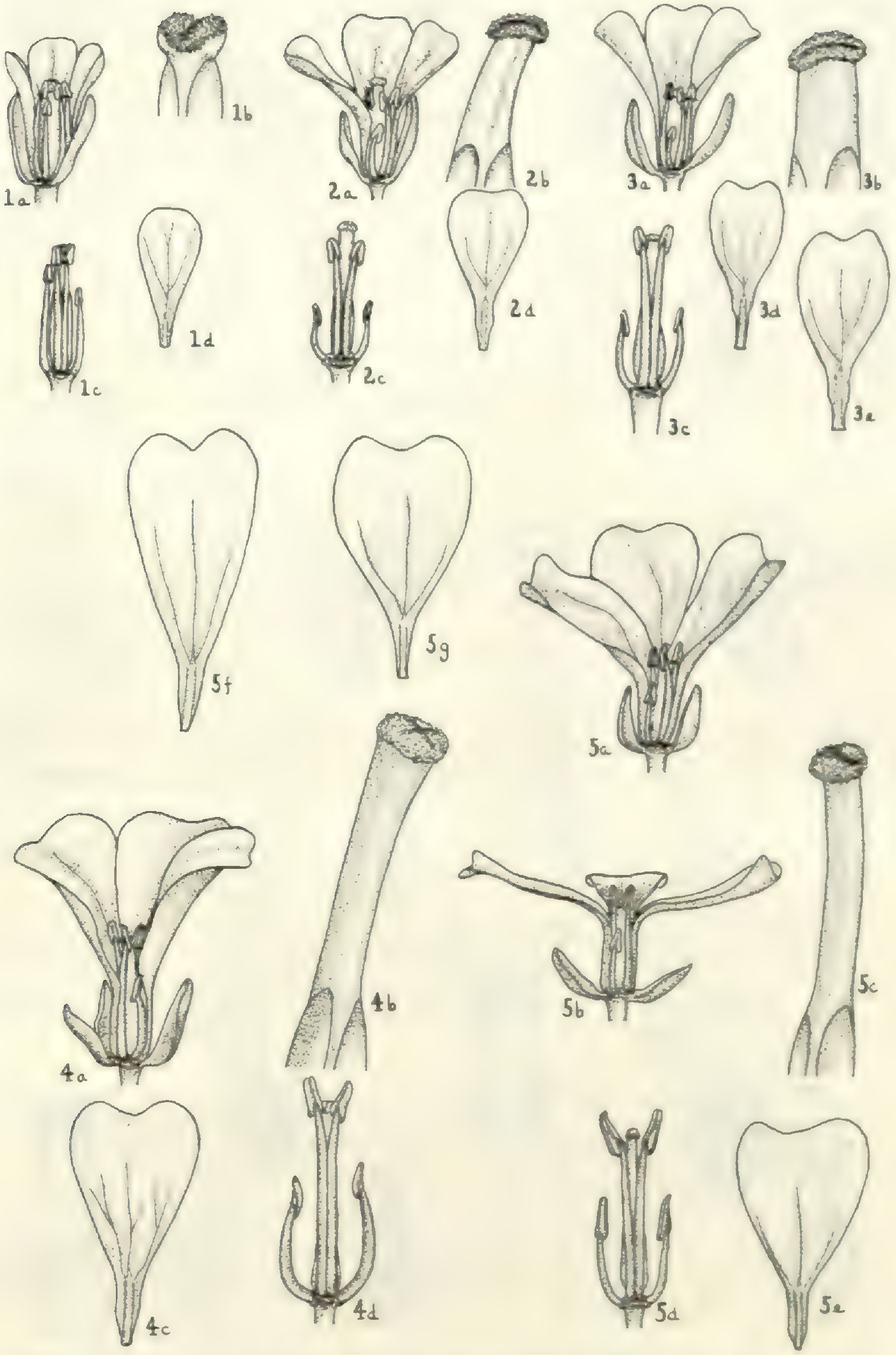

PLATE 2. Flowers and flower parts of *Leavenworthia*. Fig. 1. *L. uniflora;* 1a, flower; 1b, stigma; 1c, stamens; 1d, petal. Fig. 2, *L. exigua* var. *lutea;* 2a, flower; 2b, style and stigma; 2c, stamens; 2d, petal. Fig. 3. *L. exigua* var. *exigua;* 3a, flower; 3b, style and stigma; 3c, stamens; 3d, e, petals. Fig. 4, *L. crassa* var. *crassa;* 4a, flower; 4b, style and stigma; 4c, petal; 4d, stamens. Fig. 5. *L. stylosa;* 5a, b, flowers with different petal stance; 5c, style and stigma; 5d, stamens; 5e, f, g, petals. All flowers and petals × 2; styles and stigmas × 10; stamens × 3. Drawings by Ruth Hsu Chen.

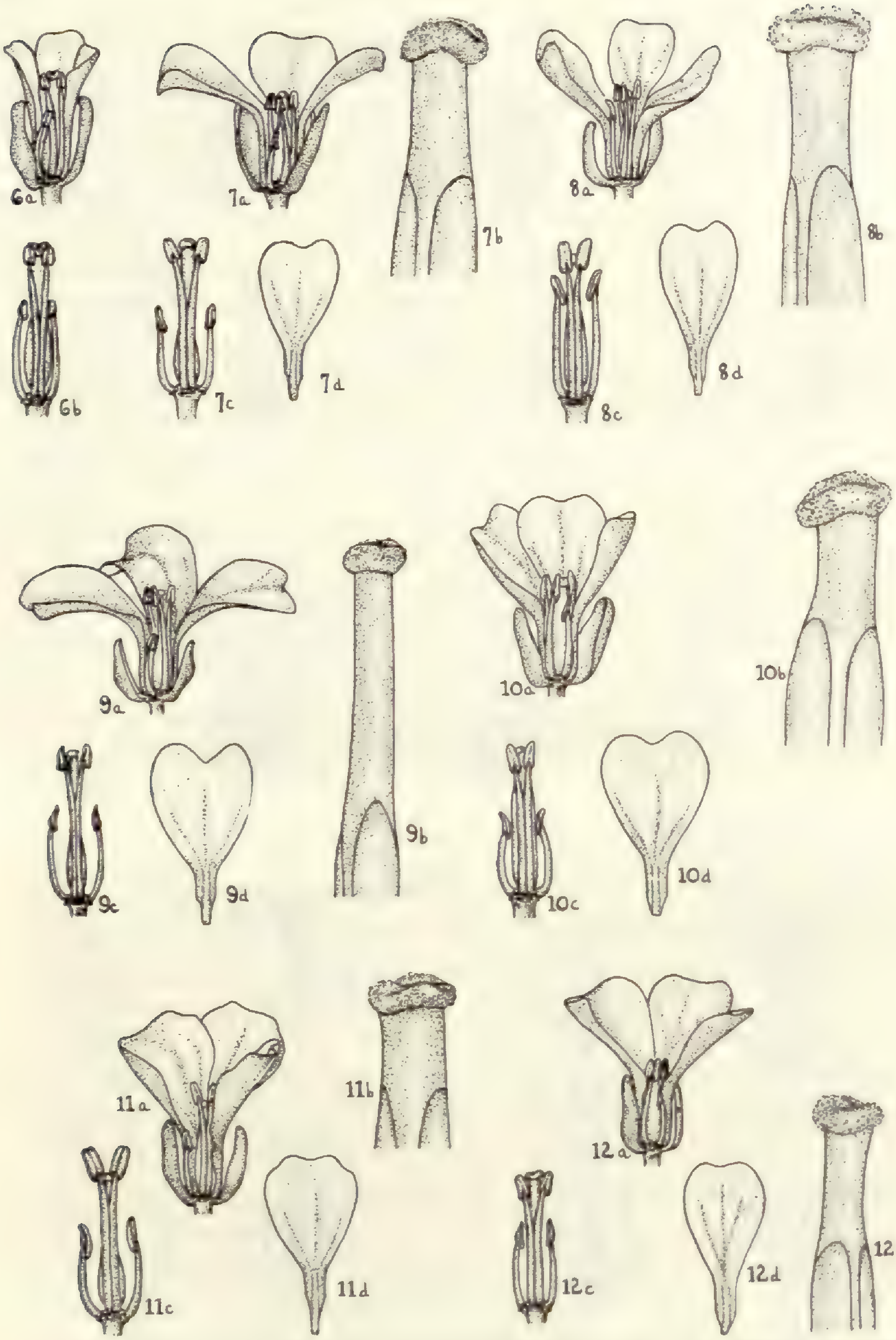

PLATE 3. Flowers and flower parts of *Leavenworthia*. Fig. 6, *L. uniflora;* 6a, flower; 6b, stamens. Fig. 7, *L. exigua* var. *exigua;* 7a, flower; 7b, style and stigma; 7c, stamens; 7d, petal. Fig. 8, *L. aurea;* 8a, flower; 8b, style and stigma; 8c, stamens; 8d, petal. Fig. 9, *L. alabamica;* 9a, flower; 9b, style and stigma; 9c, stamens; 9d, petal. Fig. 10, *L. aurea;* 10a, flower; 10b, style and stigma; 10c, stamens; 10d, petal. Fig. 11, *L. alabamica* var. *brachystyla;* 11a, flower; 11b, style and stigma; 11c stamens; 11d, petal. Fig. 12, *L. torulosa;* 12a, flower; 12b, style and stigma; 12c, stamens; 12d, petal. All flowers and petals ×2; styles and stigmas ×10; stamens × 3. Drawings by Ruth Hsu Chen.

TABLE 2. STAMEN PATTERN AND SELF-COMPATIBILITY DETERMINATION OF POPULATIONS OR CULTURES OF LEAVENWORTHIA[3]

SPECIES	CULTURE OR POPULATION NO.	SEED SOURCE	STAMEN PATTERN OF FLOWERS					SELF-COMPATIBLE
			A	B	C	D	E	
L. stylosa	59-135	Tennessee	x					—
	59-141	"	x					—
	55161	"	x					*nt*
	6009	"	x					*nt*
	6030	"	x	x				*nt*
L. alabamica								
var. alabamica	59-29	Alabama	x					—
	59-117	"	x					—
	59-173	"	x					—
	59-113	"		x				—
	59-114	"		x				—
	5929	"	x	x				*nt*
var. brachystyla	59-115	Alabama			x	x		+
	5926	"				x		*nt*
	5932	"			x	x		*nt*
	6019	"	not observed					+
L. crassa								
var. crassa	59-118	Alabama	x	x				—
	59-120	"	x	x				—
	59-121	"		x				—
	59-122	"		x				—
	5923	"		x				*nt*
	5931	"	x	x				*nt*
var. elongata	59-119	Alabama				x		+
L. torulosa	59-20	Tennessee			x			+
	59-33	"			x			+
	59-61	"			x			+
	59-152	"				x		+
	59-179	"				x		+
	59-181	"			x	x		+
	5918	"			x	x		*nt*
	5920	"			x			*nt*
L. aurea	59-1	Oklahoma			x			+
	59-2	"			x			+
	59-6	"			x			+
	59-35	"			x			+
	59-52	"			x			+

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[3] Illustrations of the five stamen patterns indicated by letters A through E are given in Figure 2. An X is used to indicate the predominant patterns found in a given greenhouse or garden culture or wild population. In the self-compatible column, a minus sign indicates predominant self-incompatibility, a plus sign indicates self-compatibility and the letters *nt* indicate that the population or culture was not tested.

Table 2. *(Continued)*

SPECIES	CULTURE OR POPULATION NO.	SEED SOURCE	STAMEN PATTERN OF FLOWERS					SELF-COMPATIBLE
			A	B	C	D	E	
	59-128	"			x	x		+
	59-170	"			x	x		+
	59-171	"			x	x		+
	60-1	"			x			+
L. exigua var. exigua	59-4	Georgia			x	x		+
	59-10	Tennessee				x		+
	59-37	"				x		+
	59-51	Georgia				x		+
	59-70	Tennessee				x		+
	59-112	"				x		+
	59-130	Georgia				x		+
	59-131	Georgia				x		+
	59-132	Tennessee				x		+
	59-133	"				x		+
	5919	"				x		*nt*
var. lutea	59-125	Alabama				x		+
	59-129	"				x		+
	5933	"				x		*nt*
L. uniflora	59-34	Tennessee				x	x	+
	59-44	"					x	+
	59-142	Alabama				x		+
	59-143	"			x	x		+
	59-145	Tennessee				x		+
	59-146	"			x	x		+
	59-177	"				x		+
	5917	"				x	x	*nt*

L. exigua, *L. torulosa* and *L. uniflora*. A sharp break in flower size separates the two groups of species.

A slight tendency towards a decrease in size is noticeable in *L. crassa* var. *elongata* as compared to var. *crassa* and a similar trend may be present in *L. alabamica* var. *brachystyla* as compared to var. *alabamica*. In these instances where var. *elongata* and var. *brachystyla* are the self-compatible components of their respective species, it would appear that flower size reduction is in the beginning stages.

Flower Odor. — The presence of a pleasant odor in the flowers of insect pollinated plants is so commonplace it is usually taken for granted. However, when some species have strongly odoriferous flowers and other species of the same genus have non-odoriferous flowers, this item becomes of interest. In checking various populations of *Leaven-*

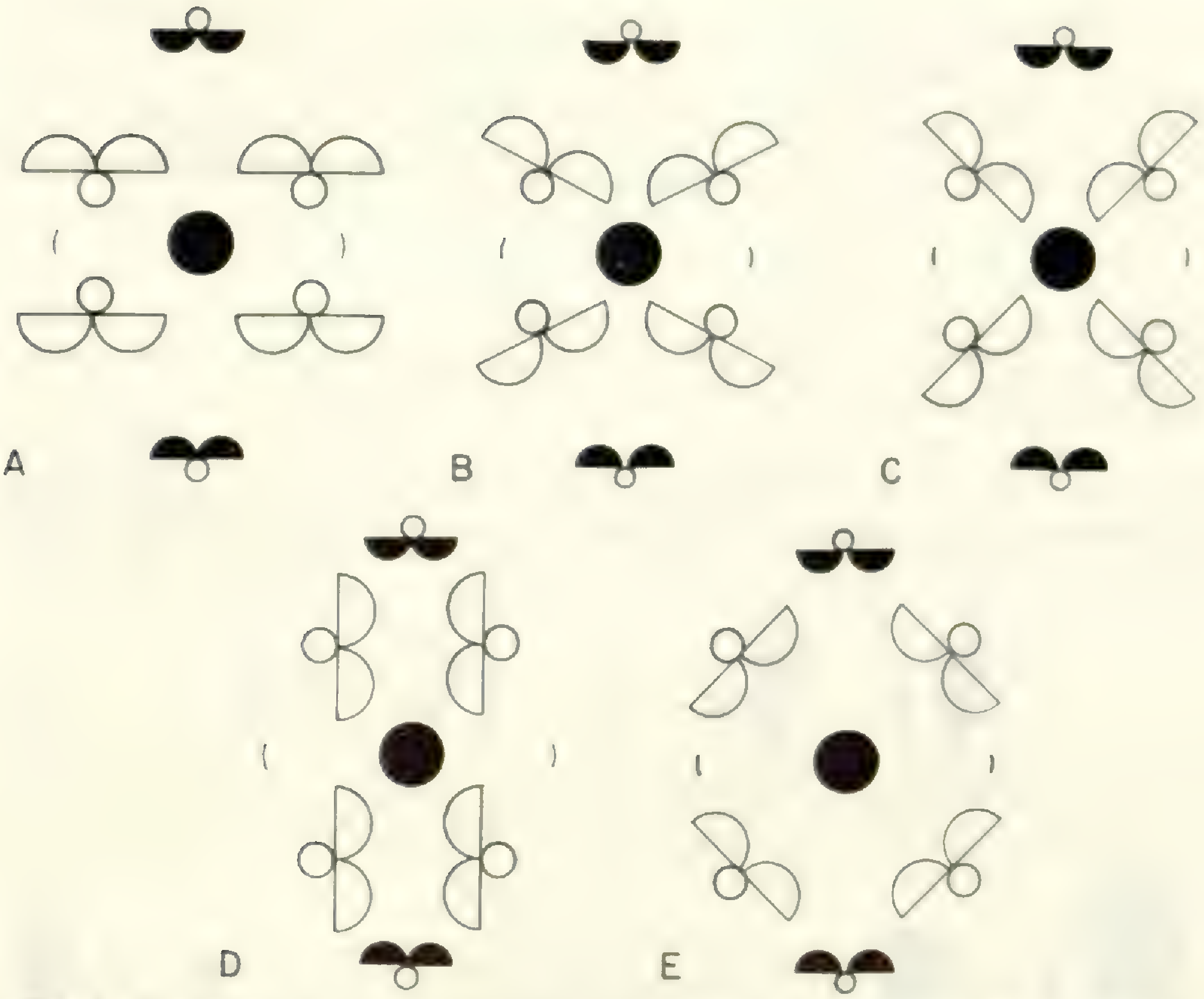

FIG. 2. **Diagrams of stamen patterns with respect to the stigma. The stigma at** center is black. The single stamens are most remote from the stigma and the bilobed anthers are shown in black with the filament in each case shown as a circle at the back. The pairs of stamens are indicated by a small bracket. The dehiscence lines of the anthers are on the rounded portion of each anther sac. Fig. 2A. The paired anthers are in an extrorse position. Fig. 2B. The paired anthers are rotated slightly. Fig. 2C. The paired anthers are rotated until the edge of one anther sac is nearly in contact with the stigma. Fig. 2D. The paired anthers are nearly in an introrse position. **Fig. 2E. The paired anthers are in a fully introrse position.**

worthia during three spring seasons, it was found that the flowers of *L. stylosa*, *L. alabamica* and *L. crassa* bear a mild, sweet scent; *L. aurea*, *L. exigua* and *L. uniflora* are non-odoriferous and variation in this respect occurs in *L. torulosa*. In some populations of *L. torulosa*, the flowers are faintly odoriferous, in others more so and in still others the flowers are wholly non-odoriferous.

It was immediately evident that odoriferous flowers characterized the predominantly self-incompatible species and that non-odoriferous flowers were a feature of the self-compatible species. *L. torulosa*, although self-compatible, has not become wholly non-odoriferous. The trend from odoriferous to non-odoriferous flowers parallels the trend from large to small flowers in both the 15-paired chromosome group of species and in the 11-paired group.

Flower Movements. — The flowers of *Leavenworthia* are very sensitive to light diminution and will completely close from a fully expanded condition if there is a shift from sunny to cloudy skies. As a natural circumstance, the flowers close in late afternoon on normally bright days and they do not open at all on continuously dull or rainy days. They may open and close several times during the course of a day when periods of brightness and dullness alternate. In the open flowers of *L. stylosa, L. alabamica, L. crassa* and to some extent in *L. torulosa,* the petal-stance differs from that of the other species. In the first group, the limb of the petal flares at right angles to the claw and the four petals together

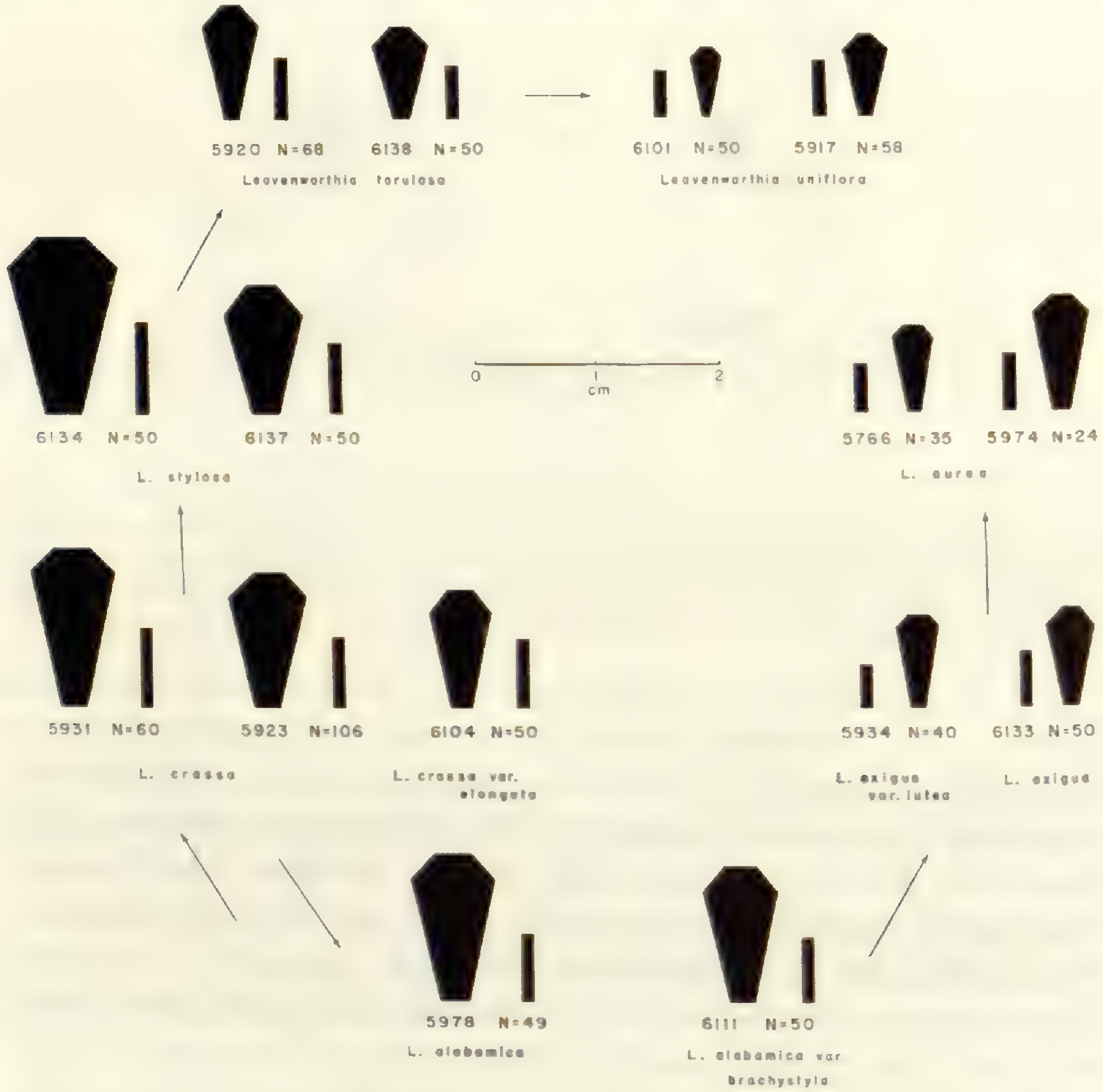

FIG. 3. Ideographs drawn to scale from means of linear dimensions of petals and sepals of *Leavenworthia*. A total of three measurements were taken on one petal and one sepal from each flower of the population sample. In each set of two ideographs, the mean length and mean width of the petals are depicted by the cuneiform ideograph and the mean sepal length by the bar ideograph. The population number and the number of samples measured are given below each set. The arrows indicate probable evolutionary direction. The population numbers are the same as collection numbers placed on specimens deposited in herbaria.

TABLE 3. PETAL AND SEPAL MEASUREMENTS OF SAMPLES FROM WILD AND CULTIVATED POPULATIONS OF LEAVENWORTHIA[4]

SPECIES & POP. NO.	NO. OF FLOWERS	PETAL LENGTH mm			PETAL WIDTH mm			SPEAL LENGTH mm			SITE
L. alabamica											
var. **alabamica**		$\bar{x}$	s	$\sqrt{\bar{x}}$	$\bar{x}$	s	$\sqrt{\bar{x}}$	$\bar{x}$	s	$\sqrt{\bar{x}}$	
5929	97	11.24	.891	.090	5.98	.309	.031	5.60	.426	.043	pasture
5978	49	11.98	1.110	.159	7.08	.988	.141	5.56	.485	.069	glade
6128	50	12.38	1.132	.160	6.97	.817	.116	6.03	.510	.072	field
var. **brachystyla**											
5926	86	11.05	.641	.069	6.82	.539	.058	5.61	.367	.040	field
5984	22	8.68	.629	.134	5.30	.591	.125	4.18	.294	.063	field
5932	65	10.78	.775	.096	6.44	.586	.073	5.34	.338	.042	field
6106	50	11.30	.562	.079	6.02	.441	.062	5.21	.351	.050	field
6111	50	11.14	.591	.084	6.03	.384	.054	5.29	.337	.048	pasture
L. aurea											
5766	35	7.05	.632	.107	3.43	.565	.096	4.18	.561	.095	greenhouse
5774	38	8.99	.599	.098	4.34	.448	.074	4.78	.252	.041	garden
5974	24	9.48	.699	.143	4.52	.521	.106	4.81	.485	.099	garden
L. crassa											
var. **crassa**											
57139	21	11.48	1.499	.327	6.74	1.380	.301	5.13	.736	.161	greenhouse
5923	55	10.83	1.147	.155	6.68	.866	.117	5.81	.499	.067	roadside
5931	60	13.13	1.037	.134	7.72	.798	.103	6.40	.594	.077	field
6102	50	12.53	1.002	.142	7.98	.869	.123	6.01	.520	.074	field
var. **elongata**											
6104	50	9.52	.685	.097	4.92	.478	.068	5.58	.434	.061	roadside
L. exigua											
var. **exigua**											
57143	26	7.43	1.074	.211	4.12	.326	.064	4.06	.215	.042	greenhouse
57149	30	7.39	.760	.139	4.08	.518	.095	4.44	.237	.043	garden
5934	40	7.56	.652	.103	3.49	.384	.061	4.91	.452	.071	garden
5997	27	7.37	.688	.132	4.22	.487	.094	4.11	.254	.049	greenhouse
5997	36	7.58	.486	.081	3.81	.467	.078	4.67	.448	.075	garden
59108	38	9.03	.667	.108	3.92	.472	.077	4.87	.445	.072	garden
5919	33	8.01	.743	.129	4.08	.535	.093	4.97	.434	.076	glade
6133	50	7.94	.513	.073	3.82	.332	.047	4.41	.282	.040	field
6139	50	7.28	.815	.115	3.29	.476	.067	4.24	.432	.061	glade
var. **lutea**											
5995	20	6.13	.320	.072	3.40	.448	.100	3.85	.235	.053	garden
L. stylosa											
55161	20	10.99	1.214	.271	6.32	1.025	.229	5.48	.559	.125	greenhouse
59105	66	10.64	.984	.121	5.81	.654	.081	5.64	.490	.060	pasture
6134	50	14.50	1.030	.146	9.13	.302	.043	7.42	.203	.029	field
6137	50	10.63	.947	.134	6.42	.883	.125	5.70	.310	.072	glade

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[4] Mean, standard deviation and standard error are given for a random sample from each population.

Table 3. *(Continued)*

SPECIES & POP. NO.	NO. OF FLOWERS	PETAL LENGTH mm			PETAL WIDTH mm			SPEAL LENGTH mm			SITE
L. torulosa											
57142	26	8.86	.914	.179	4.52	.455	.089	4.23	.364	.071	greenhouse
57142	26	7.73	.453	.089	3.60	.400	.078	4.17	.235	.046	garden
57145	20	7.77	.550	.123	3.80	.377	.084	4.43	.337	.075	garden
5918	34	10.64	.830	.142	5.89	.512	.088	5.56	.384	.066	roadside
5920	68	9.40	.870	.105	4.75	.599	.073	5.06	.560	.068	pasture
6132	50	8.90	.485	.099	4.70	.304	.043	5.14	.420	.086	pasture
6136	50	9.94	.559	.079	4.91	.995	.141	5.66	.343	.049	field
6138	50	7.68	.720	.102	4.49	.398	.056	4.24	.408	.058	glade
6150	50	9.04	.710	.100	4.76	.509	.072	5.36	.420	.086	near brook
L. uniflora											
5917	58	6.71	.581	.076	3.51	.212	.027	4.72	.397	.052	pasture
6101	50	5.84	.148	.021	2.88	.619	.086	3.93	.304	.043	field
6135	50	6.35	.537	.076	3.20	.440	.062	4.43	.463	.065	field

present a sizeable and well defined target for insect attraction and landing. This point is well illustrated in Plate 2, fig. 5b, which also shows the widely spreading sepals characteristic of the flowers of these species in full anthesis. Other species, such as *L. aurea* and *L. uniflora,* have the petals less well differentiated into blade and claw and there is a marked tendency for the petals to remain in an ascending position over their full length even at full anthesis. Plate 3, fig. 6a, shows a common petal stance found in *L. uniflora* populations of Tennessee and Alabama.

The easy movements of flower parts to a closed position insures self-pollination, at least in those flowers with introrse or partially introrse anthers, because the dehiscing part is mechanically pushed against the stigma. This is of considerable importance to species that are also self-compatible because it permits autogamy to occur under circumstances where cross-pollination may be inhibited or completely absent due to the lack of insect visitation of the flowers. As a general observation, it is more than usually evident that flower behavior in *Leavenworthia* is closely tied into the requirements of a particular species for insect pollination. For this reason, there are a large number of flower characteristics insuring insect visitation in the self-incompatible species and many of these features are modified or lost in the self-compatible species.

Observations on material grown in the greenhouse indicate that pollen ripens during the late stages of bud development and tends to be shed on the first day the flowers open. Ordinarily, the flowers will open a second day even though pollination and fertilization have occurred on the first day. If compatible pollen is withheld from the flowers, they will often open a third day, provided temperature and moisture conditions are favorable for good plant vigor.

Pollen Quality. — A broad survey of the pollens, including samples from several populations of each species and variety, revealed only that the pollen for each population was relatively uniform in size and nearly all the pollen grains stained deeply with methylene blue, indicating that very few grains (less than 1% in most populations sampled) were empty of contents. From the morphology of the pollen alone, deficiencies that might adversely affect the reproductive apparatus could not be detected. In general in interplant pollinations within the same accession, the resulting seed set was good. Also, the seed-set was good upon self-pollination in self-compatible types. Although considerable data relating to pollen quality were assembled, I cannot see that this has any real bearing upon the problems at hand as long as they revealed only that the quality was uniformly good. For this reason, the raw data are not presented. If anything but uniform results had been obtained, the data would then have been pertinent to our study.

Style Length.— There are elements of an inverse relationship between style length and silique length in *Leavenworthia.* This could be stated as, "the longer the style, the shorter the silique," or conversely, "the longer the silique, the shorter the style." However, these generalizations are only relatively applicable and do not always hold. It turns out to be a significant matter only because the long-styled, short siliques are more prevalent in the self-incompatible taxa than in those with a self-compatible breeding system. The nature of the differences may be seen by comparing fig. 1, 3 and 4 of Plate 5, photographs of fruits of self-incompatible taxa, with fig. 2, 5, 6 and 7 of the same plate. The latter are photographs of fruits of self-incompatible taxa, to the same scale.

The fact that relatively long-styled siliques more or less characterize the self-incompatible species may be interpreted as suggesting that the progenitors of *Leavenworthia* were also long-styled. This suggestion follows because the self-incompatible species are thought to be primitive in the genus. However, the point cannot be pursued because no probable progenitors of *Leavenworthia* are known and no fossil record exists.

An alternative suggestion as to the reason for a correlation of long styles with self-incompatibility lies in a consideration of pollinating efficiency. The complete dependence of the self-incompatible plants upon insects for pollen transmission places them in a vulnerable position with respect to pollination. If too few insects are active to insure an adequate supply, some of the ovules may not be fertilized. A frequent low pollen supply would set up a selective system favoring plants in which the available pollen was most effectively utilized in seed production. This might be expected to result in shorter siliques with fewer ovules. The difficulty with this interpretation is that it puts the short-fruited, long-styled species in the position of being the derived species while most of the evidence points to them as being among the primitive group.

There is good evidence that the concomitant occurrence of short styles, long siliques and self-compatibility is not wholly fortuitous. This is seen in both *Leavenworthia crassa* and *L. alabamica*, where the self-incompatible var. *crassa* and var. *alabamica* are relatively long-styled, whereas the self-compatible var. *elongata* and var. *brachystyla* have shorter styles. The general trend in the genus is shown graphically in Fig. 4.

Silique Length. — In Table 4, means of four measurements are given for the siliques of a number of populations of all species. These are length of the fertile part of the silique, excluding the style, length of style, width of silique and thickness of the silique. The length of the silique in a general way is correlated with the number of ovules produced and the possible number of seeds per silique. In Plate 5, fig. 3 and 6, the valves were removed from the siliques on the extreme right. The funiculi, slightly projecting inward from the replum may be counted to determine the number of ovules produced in each silique. In the self-incompatible *Leavenworthia crassa*, Plate 5, fig. 3, six funiculi may be seen, while in the self-compatible *L. uniflora*, fig. 6 of the

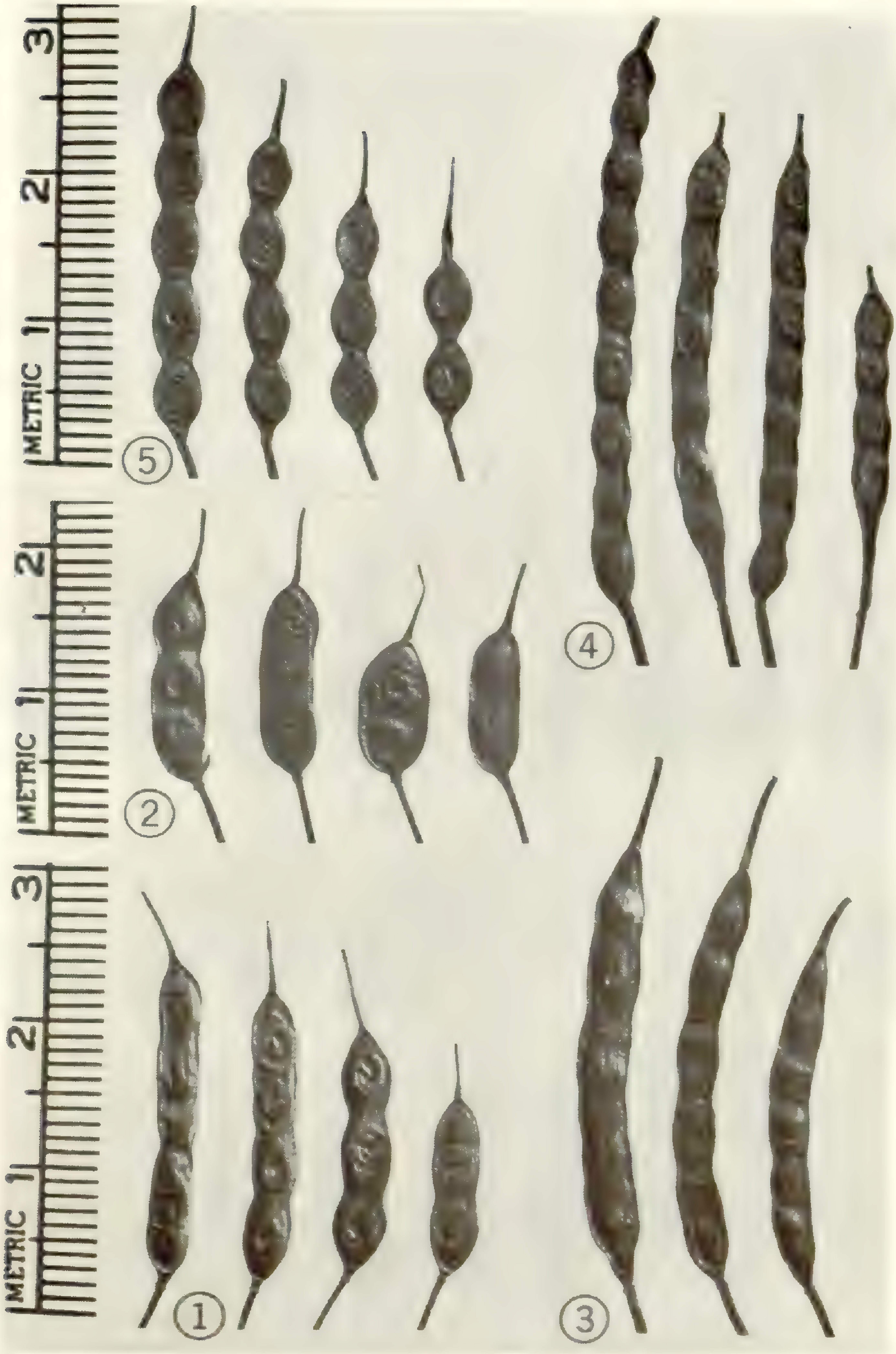

Plate 4. Siliques of *Leavenworthia*. Fig. 1-3, three fruit types of *L. stylosa* of Tennessee; Fig. 1, 1 mi. nw. Murfreesboro; Fig. 2, near Hurricane Creek; Fig. 3. 1.5 mi. east of Eagleville. Fig. 4-5, two fruit types of *L. torulosa* of Tennessee; fig. 4, 1.5 mi. east of Eagleville; fig. 5, 4 mi. ne. Shelbyville. The siliques of each figure were selected to show variation in size within a single population.

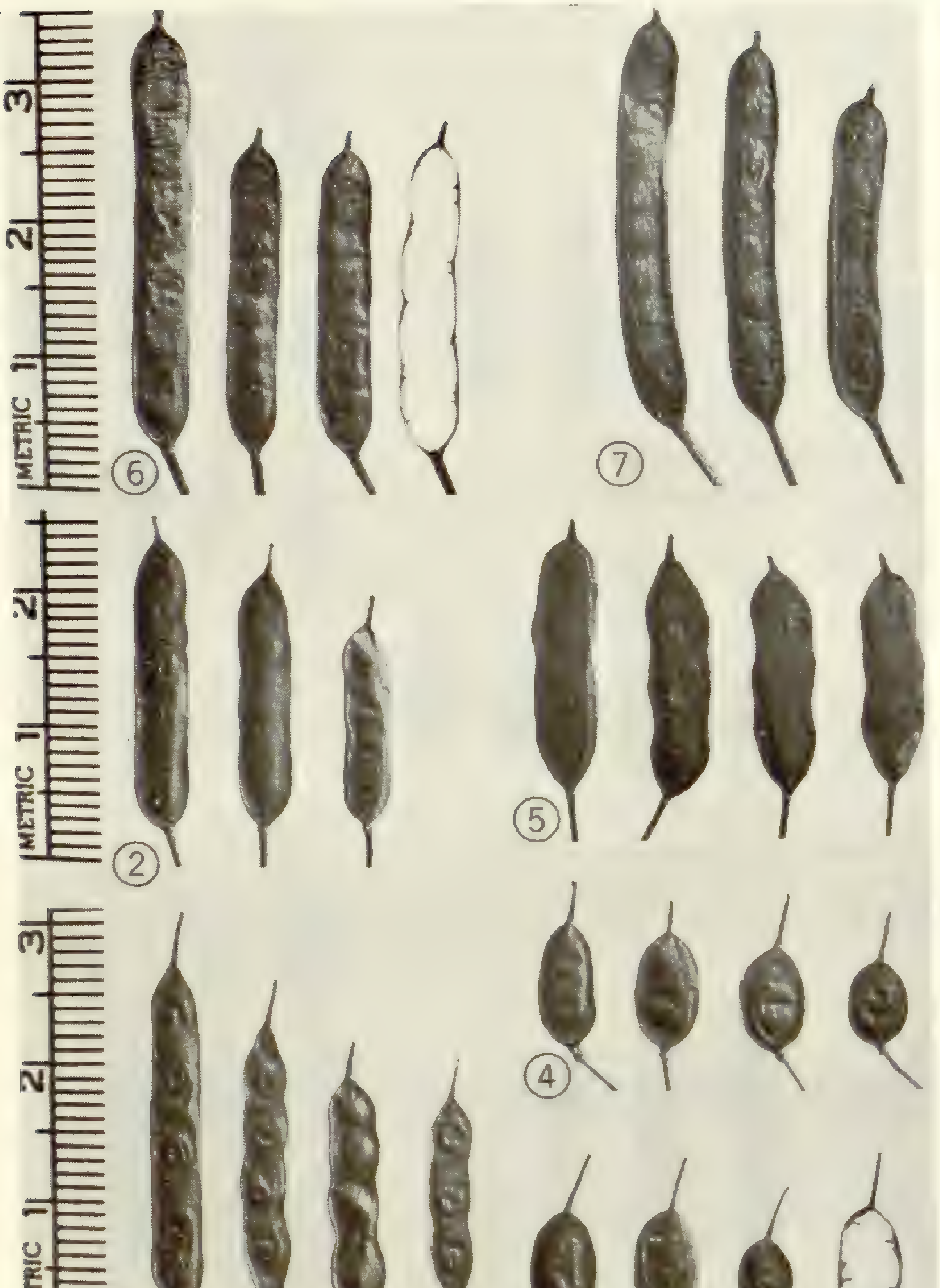

PLATE 5. Siliques of *Leavenworthia.* Fig. 1, *L. alabamica* var. *alabamica.* Fig. 2, *L. alabamica* var. *brachystyla.* Fig. 3-4, *L. crassa* var. *crassa;* in fig. 3, the silique at right has had the valves removed. Fig. 5, *L. exigua.* Fig. 6-7, *L. uniflora;* the silique at right in fig. 6 has had the valves removed. The siliques of each figure were selected to show variation in size within a single population.

same plate, seventeen funiculi may be counted. Comparing the data of Table 5, it will be seen that the number of seeds produced per silique is very significantly lower in *L. crassa*, with means of 3.3 and 6.1 in the two populations counted, than in *L. uniflora*, where a low mean of 9.6 and a high of 16.4 were found in different populations. Other species are intermediate between these two in numbers of seeds per silique.

With respect to silique length, there appear to be both

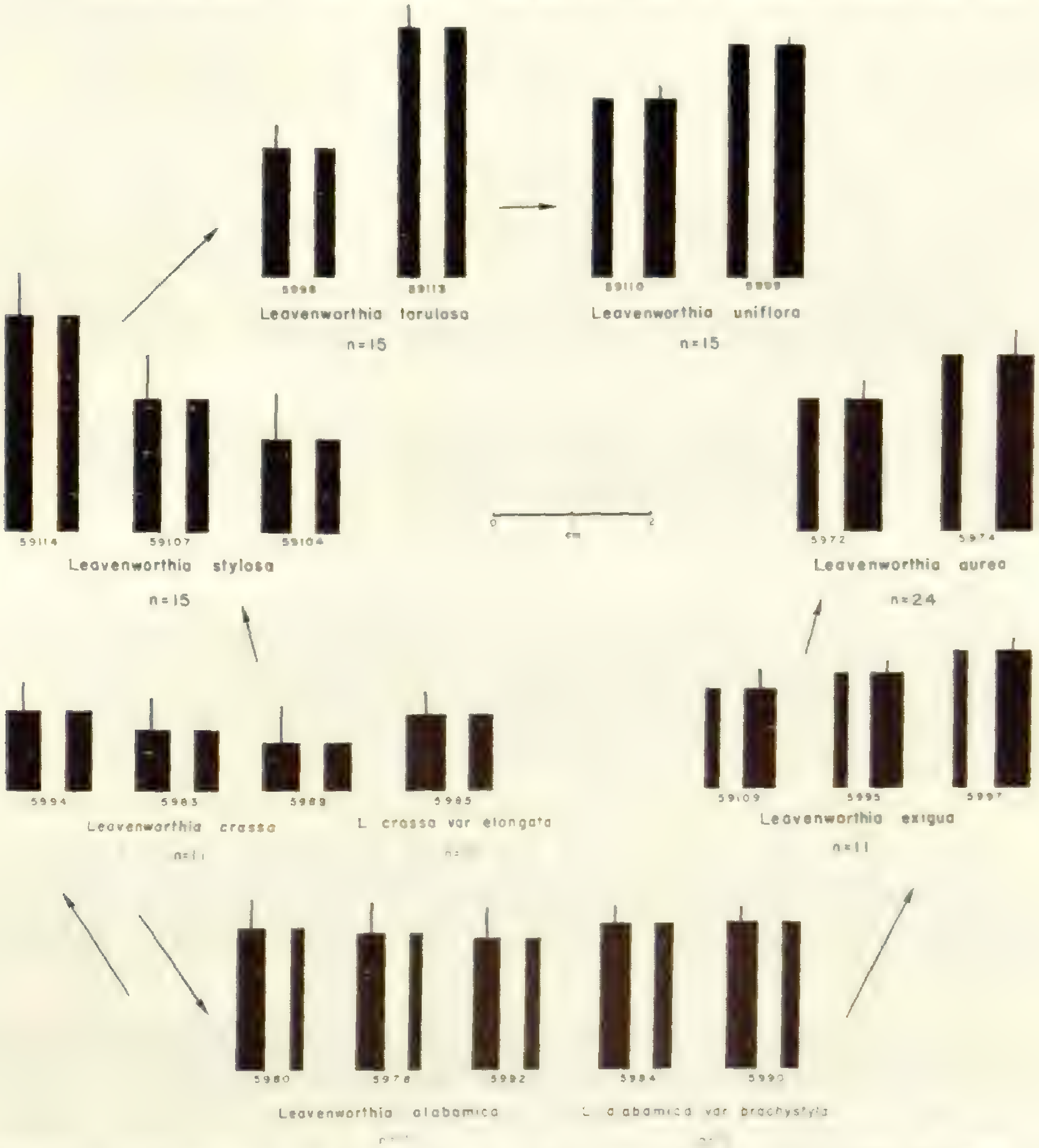

FIG. 4. Ideographs drawn to scale from the means of four measurements of siliques of *Leavenworthia*. The sample size was fifty siliques from fifty different plants of each population depicted. The bar with the thin line extension to represent the style depicts style length, silique length minus style length and silique width. The plain bar is based on mean thickness and mean silique length not including the style. The population number given below each set of two bars is also the collection number for specimens deposited in herbaria. The chromosome number of each taxon is given below the name.

within species trends and trends between species. Siliques of a certain length group are sometimes characteristic of a population or a series of populations of a particular area. In *Leavenworthia stylosa* a shorter fruited phase also is yellow-flowered and is found in the northwestern portion of the species range. For example, this phase is illustrated by populations 59104 and 6142, Table 4, where the mean silique lengths are 11.8 and 12.6 mm. respectively. A much longer fruited phase with white to light lavender flowers is found in the southern part of the species range. Here, populations 59114 and 61167, with respective mean silique lengths of 26.9 and 22 mm., are illustrative. Similar but less pronounced differences show up between *L. crassa* var. *crassa* and *L. crassa* var. *elongata*. Differences of the same order of magnitude are present in *L. torulosa*, the high mean of 31.2 mm. being nearly twice that of the low mean of 16.2 mm., but the other self-compatible species are more uniform than *L. torulosa*, as shown by the data of Table 4.

Within the three 15-paired chromosome species, trends are evident towards longer siliques with more seeds per silique. The shortest siliques with fewer seeds characterize certain populations of *L. stylosa* and although the range in both of these characteristics is quite wide in this species itself, a general trend towards longer siliques and more seeds in *L. torulosa* culminates in the largest seed producer, *L. uniflora*. The mean number of seeds produced per silique in 4 populations of *L. stylosa* was 5.9 ± 2.4, in 4 populations of *L. torulosa*, 7.7 ± 1.9, and in 6 populations of *L. uniflora*, 13.8 ± 2.2. The differences between *L. stylosa* and *L. torulosa* apparently only mark a trend but the jump in number of seeds per silique in *L. uniflora* is of undoubted significance.

A clear trend in silique length is less evident among the 11-paired chromosome species than in the 15-paired group. However, the trend towards reduction in style length is unmistakable and the combination of this with an increase in silique length appears to be a significant step within both *L. crassa* and *L. alabamica*, because it also coincides with the change from self-incompatibility to self-compatibility in these two species. This and the general situation on silique size are graphically illustrated in Fig. 4.

TABLE 4. SILIQUE AND STYLE MEASUREMENTS OF SAMPLES FROM WILD POPULATIONS OF LEAVENWORTHIA[5]

SPECIES & POP. NO.	NO. OF FRUITS	WIDTH mm			THICKNESS mm			LENGTH mm			STYLE LENGTH mm		
		$\bar{x}$	s	$\sqrt{\bar{x}}$	$\bar{x}$	s	$\sqrt{\bar{x}}$	$\bar{x}$	s	$\sqrt{\bar{x}}$	$\bar{x}$	s	$\sqrt{\bar{x}}$
L. aurea													
6152	50	4.84	.454	.064	2.56	.254	.036	16.10	2.235	.316	2.29	.299	.042
5972	56	4.81	.830	.111	2.67	.690	.092	17.54	2.40	.320	2.21	.265	.035
5973	56	4.31	.265	.035	2.56	.233	.031	20.00	2.58	.344	2.60	.271	.036
5974	56	4.67	.225	.030	2.66	.355	.047	22.29	2.74	.366	3.05	.294	.039
L. exigua													
var. exigua													
59109	65	4.10	.245	.030	1.94	.198	.024	12.65	1.653	.205	2.06	.239	.029
6143	50	3.72	.538	.076	1.17	.181	.026	14.62	1.782	.252	2.06	.174	.025
59108	64	4.53	.105	.013	1.90	.213	.026	14.88	1.915	.239	1.69	.292	.036
59100	64	4.71	.259	.032	2.18	.337	.042	15.41	2.422	.302	2.09	.283	.035
5996	60	4.65	.527	.068	2.25	.220	.028	16.32	1.921	.247	1.63	.211	.027
5997	63	4.67	.255	.032	2.33	.231	.029	17.38	1.325	.166	1.62	.256	.032
var. lutea													
5995	66	4.31	.288	.035	1.85	.177	.021	14.48	2.33	.286	1.50	.224	.027
L. alabamica													
var. alabamica													
5992	66	3.52	.298	.037	1.90	.209	.026	16.80	2.862	.352	3.72	.565	.070
5978	61	3.75	.323	.041	1.74	.226	.029	17.25	2.660	.341	3.72	.514	.066
5980	67	3.77	.329	.040	1.91	.221	.026	18.04	2.894	.353	3.50	.319	.390
6129*	50	3.62	.315	.045	1.41	.148	.021	19.34	2.335	.330	3.71	.531	.075
var. brachystyla													
61169	50	3.94	.215	.030	2.11	.490	.069	13.52	3.899	.551	2.63	.215	.030
6014*	70	3.89	.232	.027	2.17	.144	.017	14.56	1.740	.207	2.47	.302	.036
61172*	50	4.00	.165	.023	2.29	.138	.020	17.00	1.604	.227	2.24	.188	.027
5990*	68	4.09	.174	.021	2.29	.238	.028	18.60	1.881	.228	2.31	.251	.030
61170*	50	3.85	.273	.039	2.15	.217	.031	19.38	2.276	.322	2.58	.547	.077
L. crassa													
var. crassa													
5989	66	4.67	.339	.042	3.37	.430	.053	6.17	.833	.102	4.78	.554	.068
61173	50	4.97	.335	.047	3.75	.338	.048	6.67	.718	.102	4.56	.531	.075
5991	35	4.91	.497	.084	3.27	.409	.069	6.86	.944	.160	4.97	.547	.092
5983*	65	4.47	.405	.050	2.99	.338	.042	7.74	1.166	.144	3.90	.404	.050
6015*	70	4.55	.481	.057	3.71	.408	.049	8.00	1.077	.129	4.49	.250	.030
5986*	64	4.73	.313	.039	3.88	.500	.063	8.59	1.137	.142	4.91	.582	.073
5994*	37	4.33	.407	.067	2.73	.345	.057	10.03	1.344	.221	3.61	.524	.086
var. elongata													
5985	31	4.92	.262	.047	3.62	.258	.046	9.68	1.194	.214	2.84	.348	.063
L. stylosa													
59104	66	3.91	.341	.042	2.96	.312	.038	11.83	1.878	.231	5.40	.709	.087
6142	50	3.42	.487	.069	2.22	.252	.051	12.62	2.497	.353	5.26	.921	.130

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[5] Mean, standard deviation and standard error are given for each measurement in each population. A population number marked with an asterisk indicates that the population occurs in a cultivated field.

Table 4. *(Continued)*

SPECIES & POP. NO.	NO. OF FRUITS	WIDTH mm			THICKNESS mm			LENGTH mm			STYLE LENGTH mm		
		$\bar{x}$	s	$\sqrt{\bar{x}}$	$\bar{x}$	s	$\sqrt{\bar{x}}$	$\bar{x}$	s	$\sqrt{\bar{x}}$	$\bar{x}$	s	$\sqrt{\bar{x}}$
6030	70	3.53	.318	.038	2.37	.238	.028	12.95	1.861	.222	4.57	.723	.086
59105	25	4.36	.269	.054	3.06	.303	.061	14.28	3.348	.670	5.29	.719	.144
59107	47	3.65	.256	.037	2.82	.270	.039	16.72	3.174	.463	5.11	.835	.122
61164	50	3.83	.369	.052	2.71	.257	.036	16.88	3.532	.500	5.04	.936	.132
59117	47	3.55	.294	.043	2.41	.314	.046	19.17	1.110	.162	4.58	.892	.130
59118	47	3.72	.298	.043	2.64	.239	.035	20.15	1.552	.226	5.13	.358	.052
59115	47	3.44	.400	.058	2.48	.103	.015	20.30	2.843	.415	5.01	.939	.137
61167*	50	3.76	.362	.051	2.89	.310	.044	22.02	2.903	.411	5.11	.814	.115
59114*	45	3.49	.363	.054	2.69	.276	.041	26.98	4.120	.614	5.28	.539	.080
L. torulosa													
5998	64	3.60	.242	.030	2.56	.227	.028	16.28	1.035	.129	2.81	.493	.062
59111	37	2.85	.170	.028	2.42	.404	.066	16.43	2.328	.383	3.64	.321	.053
59102	50	3.13	.202	.029	2.31	.276	.039	19.84	2.454	.347	3.86	.416	.059
59101	64	3.29	.272	.034	2.53	.215	.027	21.53	3.348	.419	3.48	.428	.054
59116	47	3.22	.227	.033	2.63	.191	.028	22.51	2.726	.397	3.30	.374	.055
59106	33	3.49	.297	.052	2.83	.302	.053	23.73	3.792	.660	3.03	.576	.100
61166*	50	2.84	.249	.035	2.85	.162	.023	27.06	2.535	.359	3.60	.343	.049
59112*	25	3.02	.160	.032	2.08	.236	.047	28.80	2.848	.570	3.40	.137	.027
59113*	39	2.86	.250	.040	2.61	.887	.142	31.26	3.109	.498	2.86	.476	.076
L. uniflora													
61161	50	4.19	.282	.040	2.78	.294	.042	18.32	2.944	.416	2.31	.320	.045
61163	50	4.24	.394	.056	2.88	.257	.036	21.72	3.603	.510	1.93	.215	.030
59110	49	4.15	.267	.038	2.57	.197	.028	22.67	3.191	.456	1.53	.137	.020
59103	21	3.91	.368	.080	2.61	.271	.059	25.48	3.109	.678	1.15	.746	.163
5982	66	4.87	.261	.032	2.86	.189	.023	25.57	2.720	.335	1.18	.223	.027
6101*	50	3.97	.325	.046	2.58	.239	.034	20.70	2.660	.376	2.22	.254	.036
6126*	50	4.03	.315	.045	2.59	.237	.034	23.17	3.185	.450	2.03	.222	.031
5993*	64	4.14	.310	.039	3.09	.274	.034	25.34	2.808	.351	1.49	.295	.037
6135*	50	4.41	.451	.064	2.93	.239	.034	28.54	2.643	.373	1.12	.225	.032
5999*	39	3.81	.365	.058	2.59	.214	.034	29.31	3.163	.506	1.01	.281	.045

The interpretation of the silique length data given in Table 4 is open to some difficulties unless care is taken to discriminate between those populations growing in cultivated fields, marked with an asterisk after the population number, and those growing in less disturbed sites. Growth is nearly always more luxuriant in the old cultivated fields than in the more natural sites. The effect on silique length may be judged by comparing the data of population 61169 with population 61170 of *L. alabamica* var. *brachystyla.* Population 61169 occurs in a natural cedar glade just uphill from an old cultivated field where population 61170 is present. Obviously seeds from the glade population provided the

TABLE 5. SEED NUMBER PER SILIQUE IN WILD POPULATIONS OF LEAVENWORTHIA[6]

SPECIES &	$\bar{x}$			*s*			*Range*		
POP. NO.	M	U & A	T	M	U & A	T	M	U & A	T
L. alabamica									
var. **alabamica**									
6129	8.98	0.56	9.54	1.76	0.80	1.39	5-12	0-3	6-13
var. **brachystyla**									
5990	8.34	0.36	8.70	1.66	0.66	1.58	5-11	0-3	6-12
6014	5.56	1.20	6.76	1.91	1.01	1.32	1-10	0-6	4-10
6106	8.64	0.14	8.78	1.76	0.35	1.39	6-12	0-2	6-12
61169	5.24	0.48	5.72	1.20	0.77	1.21	3-10	0-3	4-10
61170	8.92	0.68	9.60	1.22	0.87	1.41	6-12	0-3	6-12
L. aurea									
5973	7.36	0.94	8.30	1.67	0.91	1.50	4-11	0-3	5-11
6152	5.62	1.30	6.92	1.27	1.39	1.71	3-10	0-5	4-11
L. crassa									
5994	6.18	0.32	6.50	1.32	0.55	1.25	4-10	0-2	4-10
61173	3.30	0.34	3.71	1.37	0.75	1.06	0-8	0-2	2-8
L. exigua									
var. **exigua**									
5996	5.68	0.94	6.61	1.32	0.98	1.09	3-8	0-3	4-9
5997	5.80	1.68	7.48	1.92	1.27	1.54	2-10	0-4	4-11
59108	5.48	0.96	6.44	1.42	1.25	1.26	1-9	0-7	4-9
59109	4.92	0.88	5.80	1.31	0.85	1.41	2-8	0-3	4-10
6143	6.84	0.34	7.18	1.36	0.56	1.39	5-10	0-2	5-10
var. **lutea**									
5995	6.04	0.86	6.90	1.64	0.88	1.43	2-10	0-4	4-10
L. stylosa									
6030	3.38	1.74	5.12	1.39	1.37	1.64	0-9	0-5	3-9
6142	4.78	0.46	5.24	1.40	0.84	1.53	2-8	0-4	3-8
61164	5.78	1.10	6.88	1.83	0.99	2.12	2-10	0-3	4-13
61167	9.90	1.42	11.32	1.93	1.70	1.83	5-13	0-8	6-16
L. torulosa									
69101	7.12	0.72	7.84	1.66	0.81	1.82	4-11	0-3	4-14
59111	6.56	0.52	7.08	1.42	0.81	1.65	4-11	0-4	4-12
61166	11.02	0.24	11.26	1.68	0.43	1.67	7-15	0-1	8-15
5998	6.34	0.84	7.18	1.48	0.88	1.45	4-10	0-3	5-11
L. uniflora									
5982	13.68	1.98	15.68	2.45	1.54	2.39	8-18	0-5	9-20
6101	13.90	1.08	14.98	2.29	1.05	2.30	9-19	0-3	9-22
6126	16.04	1.36	17.40	2.35	1.95	2.35	11-25	0-10	13-25
6135	16.40	1.46	17.86	2.89	1.63	2.91	4-21	0-7	12-22
61161	9.62	2.42	12.04	2.61	1.27	3.00	4-15	0-7	7-20
61163	13.42	3.06	16.48	3.04	2.18	3.80	8-20	0-10	10-25

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[6] Mean, standard deviation and range for a random sample of 50 siliques from each population are given. M = mature seeds; U & A = unfertilized and aborted ovules; and T = total, all seeds plus all ovules.

source materials for the field population and probably continues at present as a seed source. For this reason, we may assume that both populations have roughly the same genetic ingredients.

But compare the mean silique length, 13.5 mm. ±3.89 mm. of the glade population with 19.3 mm. ± 2.27 mm. found in the field population. These data were taken at the same time and under the same conditions and it must be assumed that the differences are largely, if not wholly, due to the differences between the glade site and the cultivated field. It is interesting to note that the means for silique width and thickness, and style length, do not differ significantly in the same material. It should be understood that a number of factors favorable to plant growth might be present in the cultivated fields including such items as the use of fertilizer. No attempt was made to ascertain the nature of the cultural practices in the fields where sampling was done.

Silique Width and Thickness. — Measurements of width; the dimension from replum margin across the valve and parallel to the septum to the opposite replum margin (cf. Plate 5. fig. 3 and 6), and of thickness; the dimension from the back of one valve to the back of another in a line perpendicular to the septum, were made with a thickness gauge. The plunger of the gauge could be quickly put into position and the dimension was read directly from a large dial graduated to hundredths of a millimeter.

The most important information derived from these measurements bears upon speciation and does not elucidate any particular aspect of the reproductive system. There are some differences in silique width between species but these are minimal and can be matched by similar differences between populations in such species as *L. exigua.* However, there are significant differences in silique thickness between such species as *L. crassa* and *L. alabamica.* The siliques of *L. crassa* are hard and the valves are thick walled. This feature is not seen on herbarium specimens after the siliques have become dry. On the other hand, the siliques of *L. alabamica* are flat and non-fleshy. These features are reflected in the thickness dimensions given in Table 4.

DISCUSSION AND CONCLUSIONS RELATIVE TO THE BREEDING AND REPRODUCTIVE SYSTEMS

An appropriate emphasis on the nature of the breeding and reproductive systems in *Leavenworthia* stresses the congruence of certain features with recognizable evolutionary changes that have taken place within the genus. The primary change in the breeding system itself has been from self-incompatibility to self-compatibility. It is important to point up the fact that this has taken place within two of the seven species of *Leavenworthia* and is a major trend within the genus as a whole. The most significant direct result of this change is the emancipation of a species or of a population, as the case may be, from its complete dependence upon insect pollination. The concomitant changes in the reproductive system may be attributed to new selective pressures developed because of the changed circumstances, or to the release of pressures that tended to maintain, under a self-incompatible breeding mechanism, a balanced situation involving reproductive structures, insect vectors and breeding system. The evolutionary trends affecting the reproductive system that appear to be associated with the change in breeding system are the following:

(1) Extrorse to introrse anthers.
(2) Reduction in flower size.
(3) Flaring to erect petals.
(4) Odoriferous to non-odoriferous flowers.
(5) Increase in stigma size.
(6) Decrease in anther size.
(7) Reduction in style length.
(8) Increase in ovule number.

These trends represent a remarkable set of correlations related to the shift from self-incompatibility to self-compatibility. The fact that this change has occurred independently at least three times (actually, the evidence points to a minimum of four times) indicates that powerful selective forces have been favoring self-compatibility over self-incompatibility during the recent evolutionary history of *Leavenworthia.* These same selective forces are probably continuing to act on the populations of *Leavenworthia* that today are self-incompatible.

Given the proposition that selective forces repeatedly capitalize on autogamous *Leavenworthia* plants and that they tend to fix the mechanism of release from obligate self-incompatibility into the genetic structure of the *Leavenworthia* populations, the question as to the relationship of such forces to the results produced should be asked. The matter is obviously complex and difficult to decipher. I shall attempt to deal with it first on a specific level and then on a general level.

The first assumption one has to make is that it is of considerable selective advantage to the populations of *Leavenworthia* to become self-compatible. This is in addition to the obvious fact that self-compatibility is of tremendous advantage for purposes of migration. Looking into the most vulnerable places in the reproductive cycle for clues as to why self-compatibility is of importance, we are led to look at pollination as a possible critical stage. If for any reason the supply of transported pollen is diminished or absent, this is critical to the survival of the self-incompatible populations. On the other hand, interplant transport of pollen is not a factor in the survival of self-compatible, self-pollinating populations. Since it is the transported pollen that appears to be critical, we look to the pollinating agent for further clues as to the reasons an unfavorable situation might exist.

In the case of *Leavenworthia* there is evidence that insects are not doing an efficient job of pollen transport. The evidence is largely observational and rests on the fact that in five different early spring seasons in Tennessee and Alabama, populations of self-incompatible Leavenworthias were in full bloom on many days in which insect visitation of the flowers was minimal. Had it not been for the observation at the beginning of my study that many early season plants set no fruit, I would have been tempted to assume that *Leavenworthia* was not insect pollinated, because of the general lack of insect activity on the early season flowers. It is clear that *Leavenworthia* does flower when the nights in the areas where it grows are still cool to cold and that there are numerous cold, windy or wet days when insect activity is at a minimum.

It would appear that *Leavenworthia* as a genus has somehow gotten "out of phase" with its environment as regards a critical part of its reproductive cycle, a part upon which it was highly dependent as long as it remained self-incompatible. The part, of course, was that associated with interplant pollen transport by insects. The primitive species of *Leavenworthia* are still insect-dependent and it is a fair presumption that the whole genus was at one time self-incompatible and hence insect dependent. How and why would populations of plants of a large proportion of a genus get "out of phase" with such an important factor of the environment relating as it does so closely to their success and even to their survival?

A theoretical explanation, not without basis of fact and observation, requires the assumption that all species of *Leavenworthia* are closely adapted physiologically to a particular set of edaphic conditions. These conditions, extrapolated from the particular sites where *Leavenworthia* now grows, are thought to include especially shallow soil depth over dolomitic limestone, bedded in such a way as to maintain at least temporary high moisture content near the soil surface during the wet part of the growing season. These conditions were present at all natural sites where I have observed vigorous growth of plants of the genus. High moisture, even standing water, appeared to be an essential element of the habitat. We interpret this as evidence that soil moisture was probably a feature of the early environment of *Leavenworthia* and that a close adaptation to a wet habitat has persisted as one of the requirements of these plants for survival. The requirement is genus-wide and it has not been bridged effectively during the evolutionary history of the genus down to the present. This argues for continuous high soil moisture during certain phases of the growth cycle as a limiting factor in relation to potential lines of evolutionary development that would necessitate bridging of that requirement. For example, a development that would include a dry habitat.

If we now look at the high soil-moisture requirement of *Leavenworthia* in terms of the recent geological and climatological history of the area where the genus now grows, we must conclude that the long term trend has of necessity had to be towards earlier growth and flowering. This is so because the area has gotten progressively dryer and warmer. The annual period when high moisture is available, combined with other conditions favorable for plant growth, has continuously shifted towards an earlier part of the season. It would appear that, because of its requirement for moisture, *Leavenworthia* in its growth and flowering period has followed this long term climatic trend. In doing so, because of the rigorous natural selection operative as part of the edaphic environment, the several components of *Leavenworthia,* perhaps at different times and in different places, must have reached a point in their overall evolution where the selection pressure from the habitat was of greater survival importance than the benefits of heterogamy provided by cross pollination. From this point onward, a disparity between life cycle and the role of insects in it could readily develop. Whenever the situation reached a point where flowering was critically out of phase with the presence of efficient insect vectors, an immediate premium was placed on any mutant plant that circumvented the need for insects without adversely altering other features of survival value. One common mechanism that circumvents the dependency of self-incompatible plants on insects is a shift to self-compatibility and, if necessary, to autogamy as well. It should be clear that the insects were not necessarily subjected to the same set of selective factors as the plants. There is no indication that they are specifically dependent upon *Leavenworthia* in any way. We see no reason why they should evolve to follow the same seasonal pattern as the plants.

The main step in the emancipation of self-incompatible populations of *Leavenworthia* from their dependency upon insects is the shift to self-compatibility. However, this is essentially an enabling step, permitting self-fertilization but not insuring it. Further modifications have evolved to consistently bring about self-pollination at least as a backup to whatever cross-pollination occurs. The evolutionary modifications of the reproductive apparatus relate first to the pollinating process and secondly to the exploitation of an increased and consistently abundant source of male gametes through their utilization to increase the number of fertilized ovules in each silique.

Perhaps the most important floral modifications related to the insuring of self-pollination is the shift from extrorse anthers to partially or wholly introrse anthers. This step places the anthers in the appropriate position for self-pollination but still would not insure it if the anthers were at some distance laterally from the stigma. Two further modifications are seen in the self-compatible types. One is the tendency for the anthers to be in contact with the stigma, as is characteristic of *L. uniflora* (Plate 1, fig. 8). The other is the tendency for the petals and sepals to be more erect and closer to the stigma in the self-compatible groups than in the self-incompatible groups. This, coupled with a high degree of sensitivity of the flowers to light intensity with respect to opening and closing, provides a means for mechanically pushing the introrse anthers into the stigma, thus insuring pollen deposit. On dull or rainy days, the flowers may not open at all and the pollen-charged anthers atop the elongating filaments are guided by the closed petals directly into the stigma. The rather strong evolutionary trend toward a reduction in flower size, showing up independently in both chromosome groups of the genus, may be related to these aspects of the pollinating process. A reduced diameter in the total flower size, coupled with an increase in stigma size, places the anthers and the outer floral parts closer to the outer portion of the stigmatic surface than is the case in the large flowered types. This enhances the chances of self-pollination.

The reduction in flower size may be viewed in a different way, also. It may be argued that large flowers with an open stance to the petals would be selectively maintained and enhanced by the self-incompatible groups because of their obligate position with respect to insect visitation. As soon as their dependency upon insects for pollen transport was bridged by self-compatibility, the selective pressures maintaining the large flower size would be released. Under these circumstances, flower size would tend to adjust towards a smaller size to the extent that they were previously maintained at the large size by positive selective pressures. It does appear probable, as suggested above, that the efficiency of insect transport of pollen has been of critical importance in the evolutionary history of *Leavenworthia*. However, there is no reason to reject one hypothesis and accept the other. It is probable that the release of selective pressures maintaining large flowers and the development of new ones favoring an even smaller flower than would have developed otherwise were both operational in producing the smaller flowers we now see in *L. uniflora* and *L. exigua*, for example.

The change from odoriferous to non-odoriferous flowers is probably due to the release of positive selective pressures tied up with the maintenance of an efficient pollen transport system by the attraction of insects. I have no evidence on this point except that the change has occurred. In *L. torulosa* some populations have odoriferous flowers and others do not. In the genus as a whole, it is significant that the non-odoriferous species are self-compatible and the odoriferous species are self-incompatible. *L. torulosa* is exceptional in having some odoriferous populations. I interpret the situation there as indicating that neither odoriferous nor non-odoriferous flowers are strongly selected and that the odoriferous condition is probably a remnant from the past evolutionary history of *L. torulosa*.

In considering anther size, it is clear that the largest anthers are present in the largest flowers and that reduction in size parallels a reduction in petal size and flower diameter but there is no similar reduction in sepal length or silique size. Furthermore, there is no overall reduction in pollen size. I have not determined whether fewer pollen grains are produced by the smaller anthers or not.

A reduction in style length and an increase in ovule number, along with an increase in the length of the fertile part of the fruit, appear to me to relate to an exploitation by *Leavenworthia* of an increased reliable supply of male gametes inherent in self-compatibility and self-pollination. Again, the selective pressures maintaining a particular balance between ovule number and pollen supply were undoubtedly drastically altered by a change in breeding system from self-incompatibility to self-compatibility. Among all the species of *Leavenworthia*, *L. uniflora* is the largest seed producer and it is also the most consistently autogamous. This species produces the most ovules per silique and the most siliques per plant under normal growing conditions. This results in more seeds per plant, on the average, than are produced by the plants of any other species of *Leavenworthia*. The fertile part of the silique is longer and the style is shorter in *L. uniflora* than in any of the other species. Our assessment of the reproductive apparatus as a whole, species by species, inevitably places *L. uniflora* at the top of the list as the most efficient seed producing species in the genus.

In closing this discussion, one point requires clarification or it might otherwise be misunderstood. This point relates to what might be considered by some to be a paradoxical situation in *Leavenworthia* in which all evolutionary paths seem to go from outbreeding towards inbreeding and are, in effect, leading the genus to evolutionary suicide. The latter does not appear to be wholly the case or at least the vulnerability resulting from inbreeding is slowed down somewhat in *Leavenworthia*. An important point is that although self-compatibility does permit self-pollination to effectively bring about self-fertilization, this is not an obligate process. Cross-pollination and therefore cross-fertilization may also occur and probably do, in most populations of *Leavenworthia*. In this way a sufficient degree of heterozygosity is maintained within and between populations to protect them from sudden crises occurring in their environment that might otherwise wipe them out. In annual plants such as *Leavenworthia*, a given well adapted population may build very quickly with an insured seed supply such as autogamy might provide. On the other hand, they are very vulnerable to any weak link in their reproductive cycle as compared to perennial plants, as is evident from the case at hand.

GROWTH CYCLE

The natural growth cycle from seed to flowering of all species of *Leavenworthia* is considerably longer than that required under artificial conditions. Seeds germinate in September or October producing a rosette of leaves (Plate 6) that persists in a semidormant form through the cold months of winter. Ordinarily, very little growth occurs after the last of November until the late weeks of February or the early part of March. Once temperatures are favorable, growth proceeds rapidly and flowers are produced in a few weeks time. In the field in Tennessee, we noted that *L. uniflora* and *L. exigua* tended to flower in advance of *L. stylosa* and *L. torulosa* in places where all four species occurred together. The question as to whether there were real differences in the length of the growth cycle between the species

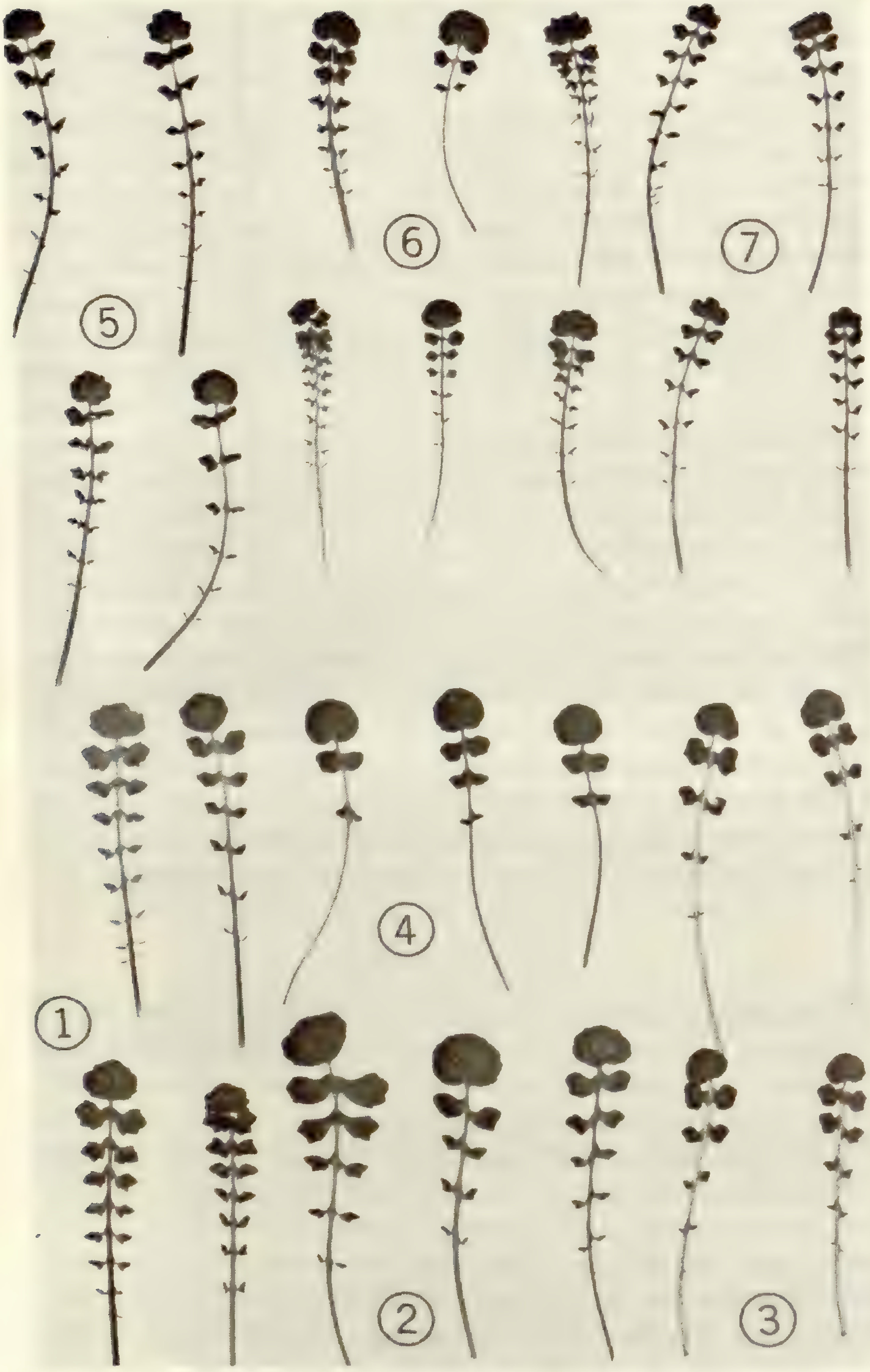


PLATE 6. Mature rosette leaves of *Leavenworthia*. Fig. 1, *L. crassa* var. *crassa*. Fig. 2, *L. alabamica* var. *alabamica*. Fig. 3, *L. exigua* var. *exigua*. Fig. 4, *L. aurea*. Fig. 5, *L. torulosa*. Fig. 6, *L. stylosa*. Fig. 7, *L. uniflora*. Fig. 1, 2, 4, 5 × 2/3; fig. 3, 6, 7 × 1/2.

was a natural one. We could not accurately check the growth cycles of the species under natural conditions but we did keep records on first flowering dates in greenhouse cultures. The pooled results are given in Table 6.

TABLE 6. SUMMARY OF GROWTH PERIOD OF LEAVENWORTHIA, 1959-60

SPECIES	CULTURES *No.*	1st GERMINATION *Date*	1st FLOWER *Date*	NO. DAYS *Range*	NO. DAYS *Ave.*
L. aurea	23	11- 4-59	3- 1-60	98-130	109
L. exigua var. *lutea*	2	11-17-59	3-15-60	103-119	111
L. exigua var. *exigua*	26	11- 4-59	3- 1-60	107-135	119
L. uniflora	8	11-17-59	3-30-60	101-142	119
L. crassa	5	11- 4-59	3-11-60	119-134	125
L. alabamica	7	11- 4-59	3-23-60	112-161	128
L. stylosa	3	11-17-59	4-12-60	124-152	141
L. torulosa	6	11- 4-59	3- 1-60	120-169	141

The lowest average number of days from seed to first flowering was found to be in *L. aurea*. This was somewhat surprising to me because in my previous experience with polyploids, particularly in *Parthenium* (Rollins, 1950), the growth cycle was slower in the high polyploids than in the lower chromosome plants. This was generally true both within species and between species of *Parthenium* insofar as the point was investigated. In the case of *L. aurea* (n = 24), the opposite situation seems to obtain. Although polyploid, it has a short growth cycle. This species is roughly comparable to *L. exigua* var. *lutea* (n = 11) in its growth cycle. These two taxa are the most southerly of the genus and appear to be related although they possess very different chromosome numbers. The effect of latitude cannot be readily assessed but it is clear that latitude as it effects climate and in turn the growth cycle is not alone responsible for the short cycle of *L. aurea* and *L. exigua* var. *lutea*. This is shown by the fact that even though the ranges of *L. exigua* var. *exigua* and *L. uniflora* are north of *L. crassa* and *L. alabamica*, they have a shorter growth cycle. If latitude were the prime factor, var. *exigua* and *L. uniflora* would be expected to have a longer growth cycle than *L. crassa* and *L. alabamica*.

It is of significance that all self-compatible species, with the notable exception of *L. torulosa*, show shorter growth cycles than the self-incompatible species. In the self-compatible species, earlier flowering, which is associated with the shorter cycle, is possible because these species are not hampered by coming into flower before insects are available to transfer pollen. By contrast, reproduction in the self-incompatible species would be seriously affected by the lack of insect vectors.

The situation in *L. torulosa*, which is self-compatible but with a long growth cycle, appears to be more complex than in the other species. The wide ranging growth cycle from a minimum of 120 days to a maximum of 169 days suggests possible wide genotypic differences. Otherwise, *L. torulosa* is closely related to *L. stylosa*, from which it presumably arose, and it might be expected to have the length of its growth cycle correspond somewhat to that of *L. stylosa*.

Geographical Distribution

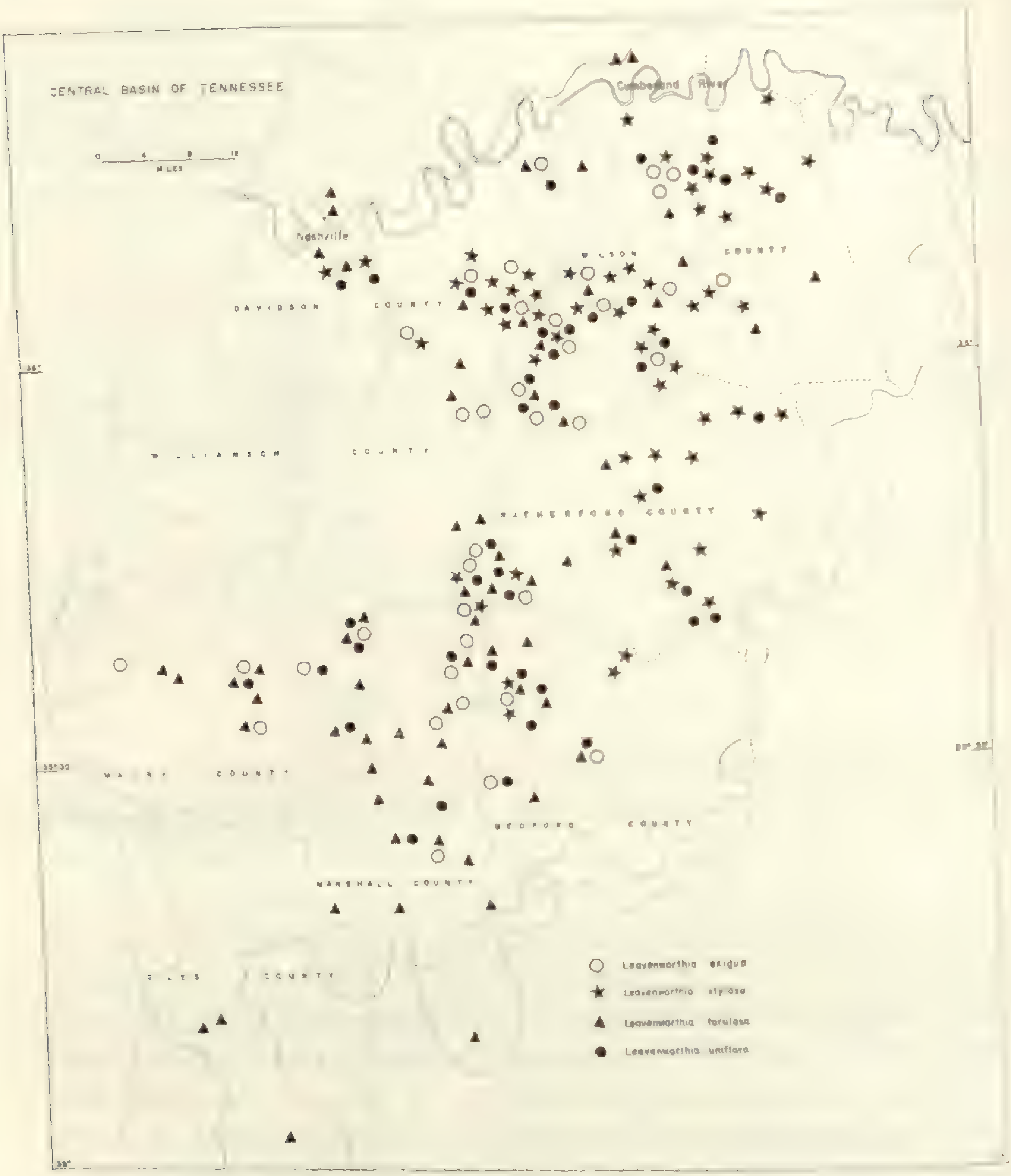
The remarkable adaptation of *Leavenworthia* to calcareous cedar glades makes locally disjunct distributions almost inevitable. These are present in nearly every species. In addition, there are some substantial disjunctions in several of the species. It is probable that these are the product of a relatively old dispersal that is presumed to have been characterized by a more continuous distribution than that of the present (Map 1). However, it is also probable that there has long been an element of habitat disjunction to be encountered in connection with the dispersal and migration of any given species of *Leavenworthia*. This in itself would place a premium upon successful dispersal by a single seed and this very likely was an important factor in connection with the repeated development of self-compatibility within the genus.

There is an interesting geographic parallel to the evolutionary picture in the genus. What is presumed to be the most basic species, *L. crassa*, is also the most restricted in its distribution. The next most restricted is *L. alabamica*, which is most closely related to *L. crassa* (cf. Map 3). Both occur only in northern Alabama. Then *L. stylosa* follows in size of geographic area and it is also the most basic species of the $n = 15$ chromosome group. In these three species we

MAP 1. Generalized distributions of the species of *Leavenworthia*.

have accounted for all that are self-incompatible. The self-compatible species, as expected, are all more widespread than the self-incompatible species. In the n = 15 group, the most widespread is *L. uniflora*. *L. torulosa* has a much smaller total range than *L. uniflora* but it exceeds that of *L. stylosa* to the north where it reaches southern Kentucky, to the southeast where it is beyond the Tennesseee River and to the south where populations are found nearly to the southern boundary of Tennessee (Map 2).

The geographical range of *L. uniflora* is marked by disjunctions particularly to the north and east of the largest area of *Leavenworthia* concentration (species and individuals) in the Central Basin of Tennessee. The one locality in Indiana, the few localities in northern Kentucky, and the few in southwestern Ohio, as well as those in eastern Tennessee are examples of substantial disjunctions in the total range. The species is presumed to have had its origin in or



MAP 2. Detailed distributions of four species of *Leavenworthia* as they occur in the Central Basin of Tennessee. The outer boundary of interruptedly exposed Ordovician limestone has been roughly shown by a solid line adapted from a progress geologic map of middle Tennessee by C. W. Wilson, Jr. (Bull. Tenn. Dept. Conserv., Div. Geol. 48: pl. 2. 1940).

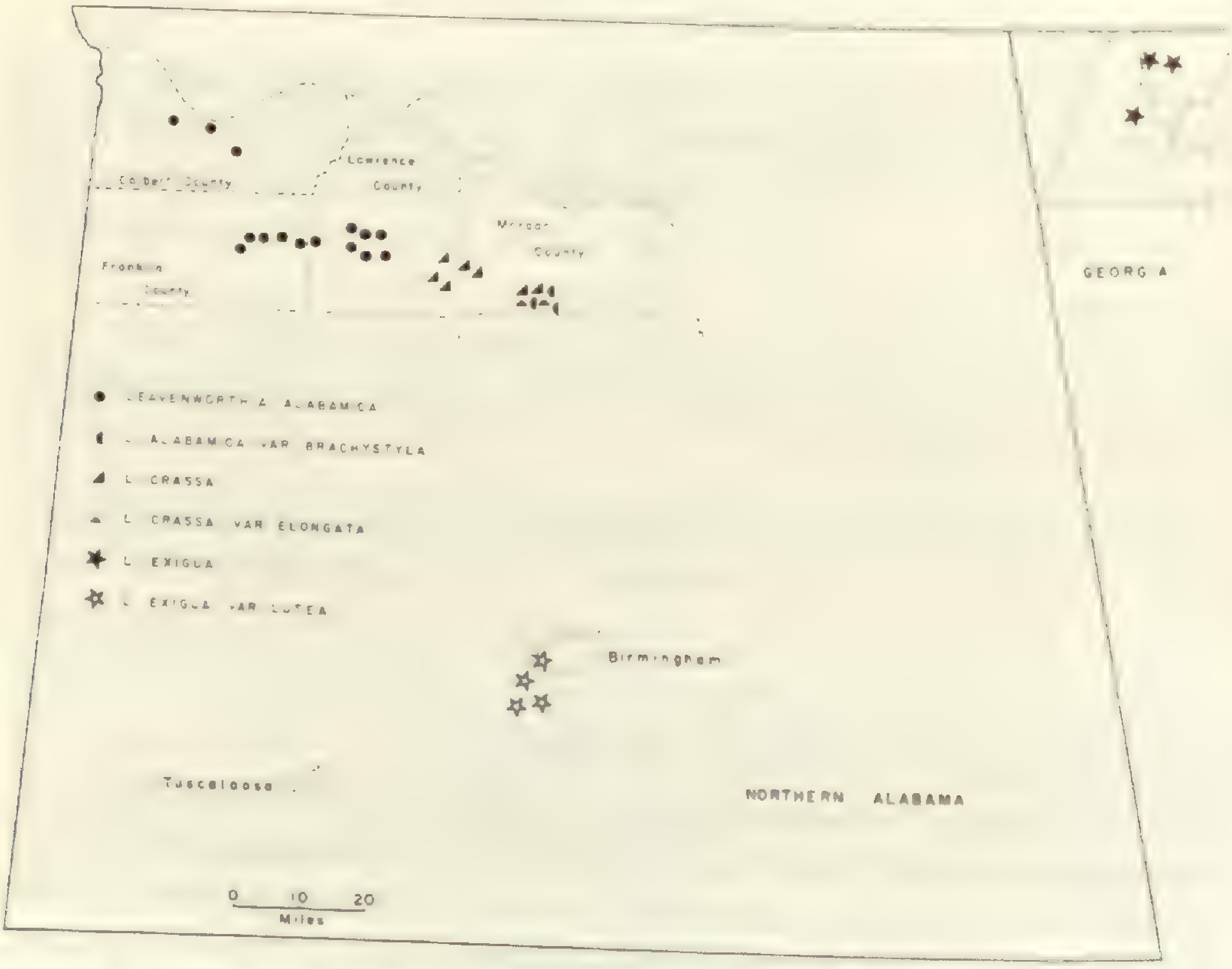
near the Central Basin of Tennessee because that is the only area where stock from which it could have arisen exists at the present time. From this general area, it has moved in all directions except directly to the west where no suitable habitats are present. The comparatively large geographical range of *L. uniflora* in an area that has largely been available for modern plant occupancy for a very long time argues for a relatively old dispersal for *L. uniflora*. Such an ancient dispersal, together with the greatest seed output of any of the species and the development of a high degree of autogamy, adequately explains the large geographical range of this species as compared to that of the other species of the genus.

Area of Origin. — Putting together what we know about evolution within *Leavenworthia*, the evidence points to northern Alabama as the area of origin for the present day species. This area also appears to be the center from which the n = 11 group of species radiated. *L. exigua* is wholly to the north, east and south of this area. Morphologically this species ties in very closely with the self-compatible *L. alabamica* var. *brachystyla*, which is present in northern Alabama. The polyploid *L. aurea*, of Oklahoma and Texas, shows close morphological ties with *L. exigua* var. *lutea* of Alabama. This connection suggests a much more southerly migration route westward for *L. aurea* than that taken by *L. uniflora* in reaching northwestern Arkansas. If *L. aurea* or its progenitors had migrated along a more northerly arc, one would expect to find some remnant populations there at the present time. Certainly, *L. uniflora* persists happily in many places in the Ozarkian region.

The n = 15 group of species shows a second pattern of migration based geographically on the Central Basin of Tennessee. If n = 11 or a number close to this is the basic stock out of which an *L. stylosa* type arose, this chromosome shift must have taken place in Tennessee. Once the n = 15 line was established it predominated over the earlier stock and then gave rise to the species of this group now present in the Central Basin area.

These suggestions as to the area of origin and the subsequent migrations of the species are radically different from those of Baldwin (1945). However, it is well to point out that he did not know anything about most of the Alabama populations at the time of his study.

Coincidence with Limestone. — The detailed mapping of *Leavenworthia* in the Central Basin of Tennessee has been carried out over a period of years at intermittent times when I have been in the field in that area. This was not done systematically over the entire land surface but each time a population was examined, specimens were taken, notes on variability were recorded and the precise location of the population was determined and recorded. These records for the four species of *Leavenworthia* growing in the Central Basin have been the basis for Map 2. In addition to the symbols indicating the location of different populations, a line roughly marking the outer boundary of Ordovician limestone, taken from a progress geologic map of middle Tennessee by C. W. Wilson, Jr., was traced. The correspondence of *Leavenworthia* distribution and the limestone is quite remarkable when the fact that a systematic mapping of *Leavenworthia* over the entire area has not been done is taken into account. It will be noted that the most restricted distribution is that of *L. stylosa.* This is the total distribution of that species as we now know it. The most widespread species within the Central Basin is *L. torulosa.* All four species occurring in the Central Basin, *L. exigua, L. stylosa, L. torulosa* and *L. uniflora,* frequently are present at the same site. Within glades, there are slight preferences by the species. If there are very wet sites and slightly dryer ones, *L. torulosa* is most apt to be found in the wettest part of



Map 3. Detailed distribution of *Leavenworthia* in Alabama and Georgia, *L. uniflora* excepted. For the distribution of *L. uniflora,* see Map 1.

the glade. *L. stylosa* also occupies very wet sites in some places but, in competition with *L. torulosa*, it is likely to be more abundant in slightly dryer sites. Both *L. exigua* and *L. uniflora* occupy dryer places in competition with the other two species. They also flower earlier and the sites where they flourish may be quite wet when they are at their flowering peak. Later these become dryer. The soil is likely to be firm and merely moist at the time the spots where *L. torulosa* and *L. stylosa* grow are still very wet.

Sympatry and Allopatry. — The area where four of the seven species of *Leavenworthia* are sympatric is in the Central Basin of Tennessee (cf. Map. 2). This is also the center of the distributional area of the genus as a whole and the area where more individuals are to be found than in any other. However, the ranges of these species are not wholly coincident even in the Central Basin. *L. stylosa*, in particular, does not occur with the other species in the southwestern portion of the Basin and *L. torulosa* is the only species I have been able to find in the extreme southern and southwestern part. The fact of sympatry cannot be disputed but we have no information on whether this represents a primary or secondary distributional development.

It seems most probable that *L. stylosa* originated in the Central Basin since it does not now occur outside. It is also possible that both *L. torulosa* and *L. uniflora* originated in the same general area although both occur outside of the Basin and may have evolved completely away from the territory of *L. stylosa*. In that case, their present sympatry with it is a secondary development. However, the geological history of the Central Basin does not preclude the possibility of sufficient isolation for speciation to have taken place around the periphery of what was earlier a limestone dome but is now the Basin. In view of the high affinity of *Leavenworthia* for wet habitats and limestone, it is likely isolation areas could develop near spring heads or stream basins where the limestone was uncovered. These could easily have been separated by some distance with rock mantle of a very different sort providing partial or complete isolation for a given population.

The presence of *L. exigua* in a sympatric alliance with *L. stylosa*, *L. torulosa* and *L. uniflora* in the Central Basin is unquestionably a secondary development. The origin of *L. exigua* is certainly traceable to the Alabama species of *Leavenworthia.*

The complete geographic separation of *L. aurea* (Map 1) from all other species of the genus, combined with the fact that this species is also polyploid is of interest. But it is of even greater interest to consider the present distribution of this species itself as a possible model for the type of geographic isolation that might have obtained during an earlier period when primary speciation within *Leavenworthia* was taking place. The Texas population is certainly effectively isolated from the population of Oklahoma and it is the uniqueness of the habitat that is the real basis for this isolation. Given such a situation, even with the populations closer together geographically, the isolation necessary to enable speciation to occur is provided. Similarly isolated populations occur in *L. torulosa, L. uniflora* and *L. exigua.*

Other allopatric distribution patterns are provided by the Alabama species of *Leavenworthia* (Map 3). *L. alabamica* and *L. crassa* are essentially allopatric although the ranges of their self-compatible varieties overlap geographically. However, where this geographic overlap does occur, the populations of the different varieties are associated with different glades and in general they are separated spatially. In exceptional situations where the different taxa meet, they hybridize as described above under the heading of interspecific hybridization.

Evolution Within the Genus

Many items with evolutionary implications have been dealt with in the preceding pages since they are intimately tied up with the breeding and reproductive systems. However, it now seems desirable to look at the evolutionary picture in *Leavenworthia* as a whole. The first matter to be considered is that of direction. Where did the evolutionary developments we now see in the genus begin and where have they led? In contemporary materials, where time sequences cannot be readily established, the direction in which the evolutionary record is read becomes a difficult matter. In many studies the best that can be done is to extrapolate from the general morphology of the groups under study and by comparative procedures try to arrive at what appears to be a reasonable evolutionary sequence. In *Leavenworthia*, where we have managed more intensive studies than can sometimes be made, we have a number of lines of evidence to draw upon.

Two evolutionary lines in *Leavenworthia* are clearly marked by chromosome number. The three species with n = 15 have a well established starting point in *L. stylosa*. The strongest evidence for this lies in the fact that it is the only self-incompatible species of the group. The large odoriferous flowers, with corollas ranging in color from yellow with an orange center through lavender to white with a yellow center, are also regarded as basic in the genus. The flower color of *L. torulosa* (white to light lavender) and *L. uniflora* (white) are represented in *L. stylosa* so that one does not have to hypothesize an outside source. However, if it were assumed that either *L. torulosa* or *L. uniflora* were basic in the group, such a hypothesis would be necessary because yellow flowers are not characteristic of any populations in either of these species. It is a logical trend from large insect pollinated flowers toward smaller flowers where insects play a lesser role in pollination, and autogamy is of increasing importance. It is clear, in my estimation, that speciation proceeded from *L. stylosa* to *L. torulosa* and *L. uniflora*. *L. uniflora* is the most highly evolved species of the three and it may have arisen from *L. torulosa* or possibly from an ancestor common to both *L. torulosa* and *L. uniflora*.

The second evolutionary line is characterized by the chromosome number n = 11. This is a group of three species with two of the three having self-incompatible components. The obviously derived species of the three is the wholly self-compatible *L. exigua*. Both *L. alabamica* and *L. crassa* are candidates for the role of progenitor of the group and the evidence is inconclusive as to which it might have been. If one examines these species from the point of view of which one possesses most completely the characters that ultimately show up in segregated form in the derived species, *L. exigua*, then *L. crassa* is favored. *L. crassa* is both white and yellow flowered and these colors show up in *L. exigua*, white being characteristic of var. *exigua* and yellow being characteristic of var. *lutea*. Also, *L. crassa* could be the source of flower color in *L. alabamica*. A further test of *L. crassa* in the role of being basic in the group is provided if the assumption is made that the n = 11 cytological group preceded the group with n = 15. This appears to be a better possibility than the other way around, as I have suggested in the discussion under the heading of cytology above. Under this assumption and with *L. stylosa* rather definitely placed in a basic position in the n = 15 group, we may then examine the morphological relationship between *L. stylosa* as the derived species and *L. crassa* as the possible primal species. Here, the situation is satisfactory. All of the distinctive features of *L. stylosa* have their counterpart in *L. crassa*. These include flower color, fruit type, style length, seed markings, and many other features.

Evidence derived from attempted interspecific crosses is of very limited value as regards interspecific relationships in *Leavenworthia*. *L. crassa* and *L. alabamica* were found to be highly interfertile but all of the other crosses gave either negative results or the F_1 hybrids produced were completely sterile. The polyploid *L. aurea* produced F_1 hybrids reciprocally with *L. crassa* but in this case as in the others the hybrids were sterile (cf. Fig. 1).

In summing up the evolutionary picture as we see it in *Leavenworthia*, we would place *L. crassa* in the role of the basic species from which *L. alabamica* and *L. exigua* form one line of development. The polyploid *L. aurea* was probably derived from these components of the genus. In particular, it would seem to have involved plants like *L. exigua* var. *lutea* in some way. The chromosome jump from *L. crassa* to *L. stylosa* is hard to understand and there is little or no evidence bearing on this problem. We have no alternative other than to assume that such a change did occur and it follows that the rest of the evolutionary history of the n = 15 group is reasonable.

Incipient Speciation. — Three different types of trends of intraspecific differentiation are readily seen in *Leavenworthia*. These include a continuous type evident in *L. stylosa*, a discontinuous geographically disjunct type found in *L. torulosa* and *L. exigua*, and a discontinuous but geographically contiguous type present in *L. crassa* and *L. alabamica*.

Although there is geographic disjunction in the other two species of the genus, *L. aurea* and *L. uniflora*, I have not detected any notable morphological distinctions between geographically isolated populations.

The continuous morphological trends in *L. stylosa* may well be a secondary situation developed from previously isolated portions of the species. The present situation is that three identifiable morphological types are present at three corners of a geographic triangle. The characteristics of these types are given below under the taxonomic treatment of the species. From the areas where each type prevails toward other areas of the triangle, there appears to be a more or less continuous modification of the distinctive features of one type toward that of the other. The situation in *L. stylosa* does not appear to be one in which there is at present any incipient speciation but rather one where speciation was well under way at some time in the past and the trend is now reversed. The previously distinctive parts of the species are now apparently in the process of fusion. Such a history for *L. stylosa* would also account for the tremendously wide range of variation now present in that species.

In both *L. torulosa* and *L. exigua*, there are wholly isolated populations that show considerable morphological divergence from the semicontinuous populations making up the main distributional areas of each of these species. A good example of a possible incipient species is the yellow flowered *L. exigua*, isolated from the rest of the species and occurring only in a limited area of north central Alabama. The Georgia populations of *L. exigua* are distinctive. In greenhouse and experimental garden cultures, plants of Georgia origin can readily be distinguished from those of Tennessee. Similar divergent isolated populations of *L. torulosa* are to be found in Kentucky and east of the Tennessee River in Tennessee. This type of isolation and ultimate divergence is to be expected in the usual speciation process and therefore it is not at all unique. But it should also be noted that isolation alone does not assure divergence in *Leavenworthia*. The best example is in *L. uniflora*. In that species, there are many glade isolated populations but the type of concomitant divergence easily seen in *L. exigua* and

L. torulosa does not show up. There are minor geographic trends in *L. uniflora* but these do not appear to be associated with any easily detected elements of speciation.

Perhaps the most interesting type of incipient speciation in *Leavenworthia* is that found in *L. crassa* and *L. alabamica.* In these species, where most of the populations in each are self-incompatible. there are certain populations on the geographic margins of their ranges that have become self-compatible and at the same time morphologically distinct. We have given these latter populations nomenclatural status because they are readily distinguishable from the bulk of *L. crassa* and *L. alabamica* in each case. Detailed descriptions of these taxa are given below.

The geographic situation differs in the two species in that the self-compatible populations of *L. alabamica* var. *brachystyla* are not in geographic contact with the self-incompatible *L. alabamica* var. *alabamica* whereas the self-compatible populations of *L. crassa* var. *elongata* are in the same geographic area as the self-incompatible *L. crassa* var. *crassa.* They are in different glades but the components of these glade systems are not wholly isolated. Evidently, evolutionary divergence has proceded in these instances without the benefit of full geographic isolation. The possibility of this happening is provided by a combination of the switch-over in breeding system and the semi-isolation of the glades. Although there is a difference in degree of isolation in each case, neither of these divergent varieties can be said to be sufficiently geographically isolated to insure genetic isolation over a long time-span.

The fact that some populations of *L. crassa* var. *crassa* and of *L. alabamica* show partial self-incompatibility without notable morphological differences from corresponding self-incompatible populations suggests that the switch to self-compatibility is an initial step in the process of intraspecific divergence. Whether self-compatibility then takes over as the dominant breeding system in any given population undoubtedly depends upon a complex of factors. However, the potentiality for this being a significant initial step in speciation is confirmed by the presence of *L. crassa* var. *elongata* and *L. alabamica* var. *brachystyla* as products of the process thus begun. Such a result is traceable to the change in breeding system and its operation against a background of partial isolation to set the speciation process into full motion.

The general importance of a situation such as exists in *L. crassa* and *L. alabamica* in the process of speciation can only be suggested to be greater than is at present recognized. Too few plant groups have been carefully examined for the role of the breeding mechanism in the initial stages of speciation to be properly evaluated on a broad basis.

TAXONOMIC TREATMENT

Leavenworthia Torrey, Ann. Lyc. Nat. Hist. 4: 87. 1837

Herbaceous glabrous annuals; early leaves simple with a slender petiole, later leaves progressively more pinnately lobed, mature leaves rosette forming and lyrately pinnatifid; early flowers borne on erect peduncles originating at the center of the rosette of leaves; later flowers, if present, occurring in loose racemes borne by true stems originating in the axils of the rosette leaves; pedicels slender, straight, divaricately ascending; sepals nearly equal, greenish, non-saccate, spreading at right angles to erect during full anthesis; petals obovate to lingulate, truncate to deeply emarginate; corolla white with yellow center, yellow with orange center, lavender with orange center, or several less defined combinations of these colors; stamens strongly tetradynamous, single stamens with anthers always introrse, paired stamens with anthers extrorse, introrse, or between these extremes; siliques with a very short gynophore, nearly sessile, flattened parallel to the septum to nearly terete or globose, fleshy in some species; funiculus free; septum with a central nerve; seeds in a single row in the silique, flattened, winged to nearly wingless, orbicular to longer than broad; seed coat with prominent reticulum of areolae; radicle of embryo short, straight to slightly appressed along margins of cotyledons; cotyledons orbicular.

TYPE SPECIES: *L. aurea* Torr.

KEY TO THE SPECIES

A. Petals emarginate, yellow, white or lavender, 7-15 mm. long; leaf-lobes entire to shallowly dentate, terminal lobe markedly larger than distal lateral lobes; radicle of embryo usually straight or bent at tip, not adpressed to edges of cotyledons except in *L. torulosa*.

  B. Siliques not torulose or only slightly so in *L. stylosa*; petals yellow, white or lavender; areolae of seed coat smaller over embryo area than elsewhere; wing-like area of seed well developed.

    C. Petals 10-16 mm. long, deeply emarginate; styles 3-7 mm. long; siliques either thick or flat.

      D. Siliques thick, fleshy; styles 3-7 mm. long (sometimes shorter in *L. crassa* var. *elongata*); petals yellow, white or lavender.

        E. Siliques 12-25 mm. long, 3-4 mm. wide; radicle of seed embryo slightly curved or sometimes straight; seed slightly elongated to nearly orbicular, cleft at one side of long axis .... 5. *L. stylosa.*

E. Siliques 6-12 mm. long, 4-5 mm. wide; radicle of seed embryo short and straight; seeds orbicular or slightly longer than broad, cleft at the basal end .... 1. *L. crassa.*

D. Siliques thin, flat; styles 3-5 mm. long (shorter in var. *brachystyla*), petals white to lavender .... 2. *L. alabamica.*

C. Petals 7-10 mm. long, shallowly emarginate; styles 1-3 mm. long; siliques flat.

F. Siliques thin, not margined; terminal leaf-lobes angular; plants of Kentucky, Tennessee, Georgia and Alabama .... 3. *L. exigua.*

F. Siliques thick, margined; terminal leaf-lobes rounded; plants of southeastern Oklahoma and eastern Texas .... 4. *L. aurea.*

B. Siliques conspicuously torulose even when young, petals white to light lavender; areolae of seed-coat nearly uniform in size; wing-like area of seed very narrow or absent ...... 6. *L. torulosa.*

A. Petals entire, white, less than 7 mm. long; leaf-lobes deeply dentate, terminal lobe only slightly larger than distal lateral lobes, radicle of embryo adpressed to edges of cotyledons .... 7. *L. uniflora*

1. **Leavenworthia crassa** Rollins, sp. nov.

Glabrous winter annual; true stems present only in well developed plants, arising in the axils of basal leaves, decumbent, unbranched, 1-4 dm. long, always bearing a loose raceme of long-pedicelled flowers; early leaves usually entire or shallowly dentate; leaves of fully grown plants homomorphic, mostly basal, lyrately pinnatifid, 3-8 cm. long, terminal lobe 0.5-2 cm. wide; lobes dentate, mostly paired, variable, terminal lobe conspicuously larger than the lateral lobes; early season flowers scapose, scapes 4-8 cm. long, later racemose flowers on slender pedicels 4-7 cm. long; sepals linear-oblong, 5-6.5 mm. long, spreading at right angles at full anthesis; petals obovate to broadly spatulate, deeply emarginate, 9-14 mm. long, 5-8 mm. wide, yellow with orange claw or white with yellow claw or with some intermediate combinations, blade spreading at right angles at full anthesis; siliques firm, globose to oblong, fleshy, 6-11 (-12) mm. long, 3.5-6 mm. wide, 2.5-5 mm. thick when fresh; styles 2.5-6 mm. long; seeds 2-8 per silique, dark brown, winged, nearly orbicular, 3-4 mm. in diameter; embryo straight or nearly so; areolae of seed-coat larger and more conspicuous on the wings and at base of wings than over the area of the seed occupied by the embryo. $n = 11$.

Herba annua; foliis radicalibus rosulatis petiolatis lyrato-pinnatifidis lobatis glabris 3-8 cm. longis; floribus scapiformibus vel cauliformibus; scapis axillaribus tenuibus glabris 4-8 cm. longis nudis 1-floribus; caulibus 1-3 foliatis axillaribus decumbentibus 1-4 dm. longis; sepalis lineari-oblongis 5-6.5 mm. longis; petalis obovatis vel late spathulatis emarginatis aureis vel candidis 9-13 mm. longis; siliques crassis globosis vel oblongis 6-11 (-12) mm. longis, 3.5-6 mm. latis; stylis 2.5-6 mm. longis; seminibus orbicularibus 3-4 mm. in diametro uniseriatis; cotyledonibus planis.

Type in the Gray Herbarium collected on thin soil over limestone, 1 mi. east of McKendry, Morgan Co., Alabama, April 4, 1959, *Reed C. Rollins 5923.*

KEY TO THE VARIETIES

Siliques 6-10 mm. long; styles 3-6 mm. long; petals white to yellow. 10-13 mm. long .... 1a. var. *crassa.*
Siliques 8-12 mm. long; styles 2.5-3.5 mm. long; petals yellow, 9-11 mm. long .... 1b. var. *elongata.*

1a. L. crassa var. crassa

Plate 5, fig. 4 & 5; Plates 7 & 8

DISTRIBUTION: southeastern Lawrence and southwestern Morgan Counties, **Alabama.** (Map 3). LAWRENCE COUNTY: 2.5 mi. west of Danville, *Rollins 5931* (GH); 8 mi. east of Wren, *Rollins and Chambers 5713; 57139* (GH); 4 mi. southwest of Danville, *Rollins 6125* (GH); 1¼ mi. southeast of Speake, *Lloyd 204* (GH). MORGAN COUNTY: ¼ mi. north of Danville, *Rollins 5983* (GH); same general locality, *Rollins and Chambers 5721; 57141; Rollins and Channell 5628* (GH); 1 mi. east of McKendry, *Rollins 5991* (GH, topotype); 1 mi. northeast of McKendry, *Rollins 5989; 61173* (GH); 3 mi. southeast of McKendry, *Rollins 5927* (GH); 5 mi. west of Falkville, *Rollins, Solbrig, Hilferty and Lloyd 6015* (GH); 3 mi. southwest of Massey, *Lloyd 268* (GH); 1½ mi. southeast of Massey, *Lloyd 299* (GH); 1 mi. southwest of Lebanon. *Lloyd 252* (GH).

1b. L. crassa var. elongata Rollins, var. nov.

Herba annua; siliquis 8-12 mm. longis, crassis; stylis 2.5-3.5 mm. longis; petalis aureis, 9-11 mm. longis.

Type in the Gray Herbarium collected in a pasture near limestone quarry, 4 mi. south-southwest of Lebanon, Morgan County, Alabama, April 6, 1961, *Reed C. Rollins 6112.*

DISTRIBUTION: southwestern Morgan County, **Alabama.** (Map 3). MORGAN CO.: near limestone sink, 6 mi. southwest of Falkville, *Rollins, Solbrig, Hilferty and Lloyd 6021* (GH); old cornfield, 1.5 mi. southeast of Massey, *Lloyd 299* (GH); 2 mi. southwest of Lebanon, *Lloyd 277* (GH); 3 mi. west of Falkville, *Rollins 5985* (GH).

The great abundance of plants of *Leavenworthia crassa* in the system of cedar glades and adjacent fields and pastures in southwestern Morgan County, Alabama, makes it difficult to understand how this species could have been overlooked for so many years. When in full flower, it is the most conspicuous plant present in many localities. There is abundant evidence that the species is made up of a highly complex series of populations, each deviating to some degree from the other. Apparently the presence of isolated or semi-isolated glades has permitted the evolutionary development of more or less distinctive populations in association with each of these glades.

It is difficult to reconstruct the primitive situation because of the widespread destruction of the original vegetation through land use. However, it is fairly obvious that the present local distribution patterns of the populations are not the same as they were prior to the agricultural and domestic use of the land by man. Fortunately, there are remnants of populations remaining in many glade sites that have not been too drastically altered. These we have been able to identify as the well-springs of a number of different population types now more widely spread into fields and pastures. In some places, plants of these differing population types are actively intercrossing to produce a broader range of recombinant characteristics than may be seen in the individual glade sites themselves.

Considering the species as a whole, there is a wide range in flower color. In some populations the flowers are white or light lavender with a yellow center. Others are yellow with an orange center. In most white or lavender-flowered populations, the admixture of yellow-flowered plants is considerable. In at least one population, 5 mi. west of Falkville, which was sampled in two different years with the same results, yellow and white flowers were present in approximately equal numbers. On the other end of the scale, yellow-flowered populations usually have few to many white-or light lavender-flowered plants present. The one exception, so far as we know, is var. *elongata*. Here the flowers are yellow.

The yellow portion of the petal blade of var. *crassa* is not wholly consistent. Usually the major part of the blade, including the deeply notched extremity, is yellow. But there are some plants with white or cream-colored bands on the blades, tips of blades, etc. It appears that petal color is inherited in a complex way in this species.

Within *L. crassa*, there is a complete range from self-incompatibility to self-compatibility in the breeding system. Some populations are predominantly self-incompatible with partial self-compatibility present while others are predominantly self-compatible with some plants being self-incompatible.[7] The populations of var. *elongata* so far tested are all self-compatible. Furthermore, the anthers are in an introrse position. It seems quite certain that the development of self-compatibility and its predominance in some populations is part of a general evolutionary trend in *Leavenworthia* and in *L. crassa* specifically this has contributed to the differentiation found within the species.

The development of facultative autogamy accompanying the inversion of the paired anthers to an introrse position and a reduction in flower size have taken place in var. *elongata*. In one small patch of plants of this variety (Pop. 5985) found in the middle of a large population of *L. alabamica* var. *brachystyla* there was no evidence of interspecific hybridization. Progeny tests of plants of var. *elongata* and of immediately adjacent plants of var. *brachystyla* did not reveal any hybrids. The progenies from plants of both varieties were unusually uniform. These results were rather unexpected because in other localities where *L. crassa* var. *elongata* and *L. alabamica* var. *brachystyla* come together, hybridization does occur and heterogeneity is found among the plants where the two varieties are in contact. A probable interpretation of this situation is that both var. *elongata* and var. *brachystyla* are largely autogamous and that within species pollination is reinforced to some extent by the slightly earlier flowering of var. *elongata*. The net result is the presence of a uniform colony of var. *elongata* in the midst of var. *brachystyla* with no evident gene interchange between the two species.

The fruit type of *L. crassa* is most similar to that of the yellow-flowered *L. stylosa* found in Davidson County, Tennessee. It is fleshy and hard when fresh. The measurements given in Table 4 indicate the extent of this thick, fleshy development in relation to other dimensions of the siliques. In var. *crassa*, when it is growing on glade sites or in relatively unfavorable places, the siliques are often nearly globose. In more favorable places, such as fields where fertilizers may have been used, or in deeper soils, the plants become larger (over a foot in diameter) and the siliques are

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[7] Mr. David Lloyd is making a detailed study of the breeding mechanism of *L. crassa*. The results will be presented at a later time.

PLATE 7. Specimens showing some of the variation in flowering material of a population (5991) of *L. crassa* var. *crassa*.

PLATE 8. Specimens showing some of the variation in fruiting material of a population (5989) of *L. crassa* var. *crassa*.

also larger and more elongate. However, in the latter, the style is also relatively long. In var. *elongata,* the siliques are even more elongate and the styles are considerably shorter.

There is a very considerable response of the plants of *L. crassa* to favorable growing sites. This is shown in Plate 8 where the smaller, few-flowered plants were collected from nearly bare rock and the more luxuriant plants were taken from adjacent deeper soils. The range from a single-flowered plant to a many-flowered plant is illustrated in the plate and, in general, this reflects the range of the site from unfavorable to favorable. The larger plant at upper left and lower right show the more elongate fruits mentioned above. The specimens shown in Plate 7 are from the type station of the species which is a relatively favorable growth site.

Aside from the difference in chromosome number between *L. crassa* (n = 11) and *L. stylosa* (n = 15), the two species show a very different and distinctive variation pattern within themselves. If fruit shape and style length alone are considered, it may be readily seen from the data in Table 4 that while the shortest fruits of *L. stylosa* and the longest fruits of *L. crassa* are somewhat comparable in size and shape, the variation trends in *L. stylosa* are all from these dimensions towards longer fruits with shorter styles and those of *L. crassa* are towards shorter fruits with longer styles.

It is not practical at this time to try to reflect taxonomically and nomenclaturally the full complexity shown by the different populations of *L. crassa.* The comparative differences observed, as indicated above, are thought to be (as with *L. stylosa*) associated with the development of different populations systems in isolated or semi-isolated glades, each major glade or glade system in effect producing a recognizably different population or group of populations.

2. **Leavenworthia alabamica** Rollins, sp. nov.

Glabrous winter annual; true stems present only in well developed plants, these arising in the axils of the basal leaves, 1-2.5 dm. long, decumbent; early leaves with a relatively long petiole and nearly entire terminal lobe, orbicular to broadly ovate in shape, leaves of fully grown plants mostly basal, lyrately pinnatifid, 3-10 cm. long, lobes subentire to dentate, terminal lobe markedly larger than the lateral mostly paired variable lobes; early flowers scapose, scapes 4-10 cm.

long; later racemose flowers on slender pedicels up to 5 cm. long; sepals narrowly oblong, 5-7 mm. long, spreading at right angles during full anthesis; petals spatulate, deeply emarginate, 10-14 mm. long, 5.5-7.5 mm. wide, blade white to light lavender, sometimes deeper lavender, spreading at right angles during anthesis, claw yellow to orange-yellow; siliques narrowly oblong, strongly flattened parallel to septum, non-fleshy, acute to rounded at base and apex, 1.5-2.5 cm. long, 3-4.5 mm. wide, 1.5-2.5 mm. thick; styles 1.5-5.5 mm. long; seeds dark brown, nearly orbicular, winged, 3-4 mm. in diameter; embryo straight, areolae of seed-coat larger and more conspicuous on the wings and at base of wings than towards center of seed. n = 11.

Herba annua; foliis radicalibus rosulatis lyrato-pinnatifidis lobatis glabris 3-10 cm. longis; floribus scapiformibus vel cauliformibus; caulibus axillaribus decumbentibus 1-2.5 dm. longis; scapis tenuibus erectis 4-10 cm. longis; sepalis lineari-oblongis 5-7 mm. longis; petalis spathulatis emarginatis; siliquis anguste oblongis compressis 1.5-2.5 cm. longis, 3-4.5 mm. latis non crassis; stylis 1.5-5.5 mm. longis; seminibus uniseriatis marginatis orbicularibus 3-4 mm. in diametro; cotyledonibus planis.

Type in the Gray Herbarium collected in a cedar glade, 1 mi. north of Cherry Hill Crossing, about 8 mi. east of Russellville, Franklin County, Alabama, April 28, 1959, *Reed C. Rollins 5980*.

KEY TO THE VARIETIES

Styles 2.5-5.5 mm. long; siliques acute above and below .... 2a. var. *alabamica*.
Styles 1.5-3 mm. long; siliques rounded above and below .... 2b. var. *brachystyla*.

2a. L. alabamica var. alabamica

Plate 9

DISTRIBUTION: Colbert, Franklin and Lawrence Counties, Alabama (Map 3). COLBERT CO.: 5 mi. west of Tuscumbia, *Rollins, Cooley and Brass 55102* (GH); about 6 mi. west of Tuscumbia, *Rollins and Channell 5641* (GH); Red Hill, 13 mi. west of Tuscumbia, *Rollins, Cooley and Brass 55106* (GH); 4 mi. southwest of Tuscumbia, *Rollins, Solbrig, Hilferty and Lloyd 6024* (GH). FRANKLIN CO.: 5 mi. east of Russellville, *Rollins 5978* (GH); 7 mi. east of Russellville, *Rollins 5549; Rollins and Chambers 57135* (GH); 1 mi. south of Newburg, *Rollins, Cooley and Brass 5598* (GH); Isbel, *Rollins, Cooley and Brass 55101* (GH); north of Isbel, *R. M. Harper 3876* (GH). LAWRENCE CO.: ½ mi. east of Landersville, *Rollins and Chambers 5713; 57137* (GH); 5 mi. northeast of Landersville, *Rollins 6128* (GH); 4 mi. west of Moulton, *Rollins 5543; Rollins and Chambers 5712* (GH); 3 mi. south of Hatton, *Rollins and Channell 5642* (GH); western border of Lawrence Co., *Rollins and Channell 5633* (GH); 2 mi. west of Mt. Hope, *Lloyd 923* (GH).

2b. L. alabamica var. brachystyla Rollins, var. nov.

Herba annua; siliquis compressis enervatis obtusis 1.5-2.5 cm. longis; stylis 1.5-3 mm. longis.

PLATE 9. Specimens showing characteristics of plants and some of the variation in a population (5980) of *L. alabamica.*

Type in the Gray Herbarium collected in a pasture in a cedar glade area, 4 mi. southwest of Falkville, Morgan County, Alabama, April 26, 1960, *Reed C. Rollins, Otto T. Solbrig, Frank Hilferty and David Lloyd 6019.*

DISTRIBUTION: scuthern Morgan County, **Alabama** (Map 3). MORGAN CO.: 5 mi. south southeast of McKendry, *Rollins 61169, 61170* (GH); 3 mi. southwest of Falkville, *Lloyd 685; Rollins 5926; 598* (GH); 3 mi. south southeast of Massey, *Lloyd 275, 288, 290* (GH); 0.8 mi. east of Lebanon, *Rollins 61172* (GH); about 5 mi. west of Falkville, *Rollins 5932, 5990* (GH).

The relatively long styles on the fruits of *L. alabamica* naturally led early botanists handling limited and scrappy material to refer this to *L. stylosa*. The same interpretation has come down to the recent past as indicated by the distribution map (fig. 8) of Baldwin (1945). Unfortunately, Baldwin did not have growing material of *L. alabamica* as he did of several of the other species or he surely would have discovered that the chromosome number is n = 11 instead of n = 15, as he found in *L. stylosa*. In general, the style length is considerably shorter in *L. alabamica* than in *L. stylosa* but a more important difference is in the fleshiness of the silique. This characteristic is not observable in herbarium specimens. However, in fresh plants, the siliques of *L. stylosa* are thick, fleshy and firm, whereas in *L. alabamica* they are relatively thin and non-fleshy. In this respect the siliques of *L. alabamica* are more like those of *L. exigua* than any other species of the genus. The measurements given in Table 4, made on fresh material, show the basis for the above statement.

The pattern of differentiation within *L. alabamica* is perhaps less complex than that found in *L. crassa* but there are some marked trends that are readily observable. The most striking is in the breeding mechanism. In most of the populations of var. *alabamica* tested, including some from both Franklin and Lawrence Counties, self-incompatibility predominates. On the other hand, self-compatibility is the rule in var. *brachystyla*. The results of self-compatibility tests are given in Table 2. A more recent result, found by David Lloyd, shows at least one population of var. *alabamica* to be somewhat self-compatible. Undoubtedly a more exhaustive study of this species as a whole would show a more complex situation than is at present known. Our interpretation is that there is an evident evolutionary trend from self-incompatibility towards self-compatibility presently going on within the species. This trend has culminated in a high degree of self-compatibility in var. *brachystyla,* where a parallel change of the anthers of the paired stamens to the introrse position has produced the appropriate circumstances for facultative autogamy to occur. Our naming of the self-compatible populations of Morgan County as var. *brachystyla* is a recognition of the culmination of this trend but should not be assumed to indicate that we are not aware of intermediate stages in the trend itself, particularly in the most easterly populations of var. *alabamica.*

The most northerly populations of var. *alabamica* in Colbert County are distinguishable from the plants of the Franklin County area which are in turn slightly different from those of Lawrence County. Again, as in *L. stylosa* and *L. crassa,* there appears to have been prolonged isolation or semi-isolation between the major glade systems in the region and each of these has spawned a series of populations of *Leavenworthia* slightly different from the others. In the territory of *L. alabamica,* one can distinguish four such glade systems, each with several to many individual glades that are semi-isolated in themselves. The most disrupted area and the one with the smallest glades is the glade system west and southwest of Tuscumbia in Colbert County. These are only one level up from the Tennessee River and are at a lower elevation than the glade system centered just to the east and southeast of Russellville in Franklin County. The latter is toward the Bankhead National Forest which occupies a low plateau to the south. Extending from this plateau towards the Tennessee River in scallop-like fashion are low ridges that cover the underlying limestone with a mantle of soil. One such ridge separates the Russellville glade-system from the one centering on Landersville in Lawrence County. A similar low relief exists between the Lawrence County glades and those of Morgan County where var. *brachystyla* abounds.

Flower color in the various populations of *L. alabamica* does not show the kind of variation found in *L. crassa* and *L. stylosa.* In fact, yellow-flowered plants are extremely rare, having been seen in only two populations and then only a plant or two. It is probable that these observed cases represent mutants that have arisen sporadically and rarely. A comparable situation is present in *L. torulosa* where, in only one of the numerous populations I have examined, there were less than a half-dozen yellow-flowered plants.

In many populations of *L. alabamica*, the predominating flower color is white with a yellow center. In these, the color changes to light lavender as the flowers close in response to the diminished light of late afternoon or of deeply overcast skies. This is due to the fact that the upper surface of the petal limb is white and the lower surface is light lavender. When the petals are fully extended, the white surface is presented but when the petal closes to the erect position, the lavender back of the petal becomes visible. In a few populations the lavender is somewhat more intense than in the majority. An interesting situation was observed in several populations where the upper surface of the petal limb was light lavender and the lower surface was white. The fact that whole populations, consisting of hundreds of thousands of plants, bore a similar petal-color pattern suggests that some adaptive significance to it must exist but I am not able to suggest what this might be. There were no easily seen differences in the type of habitat or in the geographic continuity of one petal-color pattern as compared to the other. Adding to the puzzle is the fact that the same situation occurs in *L. torulosa*, except that a light lavender upper surface of the petal limb with a white lower surface predominates in most of the populations and in only a few populations is the upper surface white and the lower light lavender. Here the predominant color pattern is reversed from that of *L. alabamica*.

L. alabamica × L. crassa

Of all attempted crosses between species of *Leavenworthia*, the only really successful one involved the two species above. Also, where *L. alabamica* var. *brachystyla* comes into contact with *L. crassa* in Morgan County, hybridization occurs. Insofar as our present knowledge goes, natural interspecific hybridization occurs only in that area. Both *L. crassa* var. *crassa* and var. *elongata* appear to be involved in crosses with *L. alabamica* var. *brachystyla* but truly hybrid swarms are rare.

What we have seen most frequently is a thin band of what appear to be F_1 hybrids along the contact line between the two species. In general the species themselves remain unadulterated at only a short distance of a few meters away from the line of contact. At the present time we do not know whether genetic factors tend to reduce or eliminate potential introgressants or whether the particular areas of contact studied are relatively new and the opportunity for a more normal hybrid situation has not had time to develop. The sites where hybridity appears to be most prevalent are fields or disturbed pastures. We have not seen any evidence of interspecific hybridization on undisturbed land.

Some herbarium collections of hybrids of *L. alabamica* × *L. crassa* are the following, all from Morgan County, **Alabama:**

1. **L. alabamica** var. **brachystyla** × **L. crassa** var. **crassa.** — 1¾ mi. southeast of Massey, *Lloyd 917* (GH); 3 mi. southeast of Massey, *Lloyd 703* (GH); 1½ mi. east of Massey, *Lloyd 29* (GH); near Harrin Creek, 2 mi. south of McKendry, *Rollins 6122* (GH).

2. **L. alabamica** var. **brachystyla** × **L. crassa** var. **elongata.** — ¼ mi. southwest of Lebanon, *Lloyd 254; 255* (GH); 1½ mi. south of Lebanon, *Rollins 6110* (GH).

3. **Leavenworthia exigua** Rollins, Rhodora 58:75. 1956

Glabrous winter annual; early leaves with a remote shallowly dentate terminal lobe, leaves of fully grown plants lyrately pinnatifid, 1.5-5 (6) cm. long, lobes shallowly dentate, terminal lobe markedly larger than lateral lobes; early and mid-season flowers scapose, scapes 3-6 cm. long, later flowers often borne on lateral decumbent branches; young buds pendant, older buds erect; sepals nonsaccate, linear-oblong, divergent to erect during anthesis, greenish to light lavender, 3.5-5.5 mm. long; petals lingulate to spatulate, shallowly emarginate, 6-9 mm. long, 3-4.5 mm. wide, blade white to light lavender, upper claw yellowish; petals yellow in var. lutea; siliques strongly flattened parallel to septum, non-fleshy, obtuse above and below, oblong, 1-2 cm. long, 3.5-5.5 mm. wide, 1.5-2.5 mm. thick when fresh; style 1-3 mm. long; gynophore evident, nearly 1 mm. long; seeds 4-10 per silique, winged, nearly flat, irregularly orbicular, 3-4 mm. in diameter, areolae of seed-coat reticulum much smaller over embryo than in wing area; radicle straight; cotyledons orbicular. n = 11.

KEY TO THE VARIETIES

Petals white to light lavender, plants of Kentucky, Tennessee and Georgia.
  Styles 1-2 mm. long, sepals light lavender, plants of Tennessee and Georgia .... 3a. var. *exigua*.
  Styles 2-3 mm. long, sepals green, plants of Kentucky .... 3b. var. *laciniata*.
Petals yellow, plants of Alabama .... 3c. var. *lutea*.

3a. L. exigua var. exigua

Plates 10 & 11

Type in the Gray Herbarium, collected in shallow soil of glade, 1 mi. north of the North Fork of the Duck River, southeast of Unionville, Bedford County, Tennessee, April 3, 1955, *Reed C. Rollins 5535.*

DISTRIBUTION: Central Basin of Tennessee; northwest Georgia (Map 1). **Tennessee.** BEDFORD CO.: west of Shelbyville, *Sharp, Felix and Adams 11244* (GH); 1 mi. southeast of El Bethel, *Rollins 59100* (GH). DAVIDSON CO.: west of Couchville Pike, *Svenson 7715* (GH, mixture with *L. uniflora*); 1.5 mi. east of Una, *Rollins 6139* (GH); 2.4 mi. north of Lavergne, *Rollins and Chambers 5744* (GH); south of Nashville, *Shanks and Sharp 383* (GA, GH, MICH, NY, US). MARSHALL CO.: 6 mi. southeast of Eagleville, *Rollins 6133* (GH); 2 mi. south of Chapel Hill, *Rollins and Chambers 5729* (GH); 1.5 mi. north of Chapel Hill, *Rollins 59109* (GH). MAURY CO.: 4 mi. west of Pottsville, *Rollins, Solbrig, Hilferty and Lloyd 6027* (GH); 6 mi. north of Culleoka, *Rollins 5328* (GH); 3 mi. northeast of Chapel Hill, *Rollins and Channell 5663* (GH); 1 mi. north of Rally Hill, *Rollins 5919* (GH). RUTHERFORD CO.: 5 mi. north of Jerusalem Church, *Rollins 6143* (GH); 2 mi. south of Lavergne, *Rollins and Chambers 5742* (GH); 3 mi. south of Lavergne, *Rollins and Channell 5617* (GH). WILLIAMSON CO.: 3 mi. east of Nolensville, *Rollins and Channell 5619* (GH); Rocky Spring road, 2 mi. east of Nolensville, *Rollins 5512* (GH). WILSON CO.: 2 mi. west of Lebanon, *Rollins, Solbrig, Hilferty and Lloyd 6007* (GH); 3 mi. south of Gladeville, *Rollins and Chambers 57149* (GH); Lebanon, *Lloyd 413* (GH). **Georgia.** CATOOSA CO.: 2 mi. east northeast of Fort Oglethorpe, *Duncan, McDowell and Runyon 12124* (GA, GH); 1.9 mi. east of Fort Oglethorpe, *Duncan and McDowell 12235* (GA, GH); 1 mi. east of Fort Oglethorpe, *Rollins and Chambers 5704* (GH); 2 mi. east of Fort Oglethorpe, *Rollins and Channell 5650* (GH); eastern entrance to Chickamauga — Chattanooga National Military Park, *Rollins and Chambers 5702* (GH); same locality, *Rollins 5997* (GH). WALKER CO.: 11 mi. north of LaFayette, *Rollins 5996* (GH); same locality, *Rollins and Chambers 5705* (GH).

3b. Leavenworthia exigua var. laciniata Rollins, var. nov.

Herba annua, sepalis viridis, siliquis 1.5-2 cm. longis, 3-4 mm. latis, stylis 2-3 mm. longis.

Type in the Gray Herbarium, flowers white with light yellow throat, paired stamens introrse; thin soil over limestone, cedar glade, south of the Salt River, 6 mi. east of Sheperdsville, Ridge Road, 2 mi. north of state route No. 480, Bullitt County, Kentucky, April 1, 1962, *Reed C. Rollins 6201.*

DISTRIBUTION: Bullitt County, **Kentucky** (Map 1). Open field, Ridge Road, March 27, 1954, *H. A. Korfhage 2* (Univ. of Louisville).

3c. L. exigua var. lutea Rollins, var. nov.

Plate 12

Herba annua, petalis luteis, siliquis planis.

Type in the Gray Herbarium; flowers golden yellow, pasture among

PLATE 10. Specimens showing characteristics of plants and variation in a population (5744) of *L. exigua* var. *exigua* of Tennessee.

PLATE 11. Specimens showing characteristics of plants and some of the variation in a population (5650) of *L. exigua* var. *exigua* of Georgia.

cedars, 1 mi. northwest of McCalla, Jefferson County, Alabama, April 3, 1956, *R. C. Rollins and R. B. Channell 5643.*

DISTRIBUTION: Jefferson County, **Alabama** (Map 3). Western edge of Bessemer, *Rollins 5933* (GH); Bessemer, *E. J. Palmer 38975* (GH, US); 1 km. north of McCalla, *R. T. and E. R. Clausen 5760* (NY, UC); 1 mi. northeast of McCalla, *G. Cooley and F. Harper 4524* (GH); 3/4 mi. northeast of McCalla, *R. M. Harper 3834* (GH, NY, US).

The numerous populations of *L. exigua* in the Central Basin of Tennessee and those of northwestern Georgia vary little in flower color. The main portion of the petal is most frequently white but may be light lavender in many populations. A yellowish band on the upper claw of each petal gives the flower a yellow center. All yellow-flowered populations are found in the Bessemer and McCalla areas of Jefferson County in north central Alabama. These we have designated var. *lutea.* Ever since the establishment of the genus *Leavenworthia* by Torrey (1837), who referred material from Jefferson County, Alabama, to *L. aurea*, the presence of these yellow-flowered populations has been one of the main bases for a misunderstanding of *L. aurea.* These plants do resemble those of *L. aurea* in many respects but the chromosome number is $n = 11$ instead of $n = 24$. Actually, the thin, similar siliques and angular leaf-lobes, together with the same chromosome number, show unequivocally that, although yellow-flowered, these Alabama plants belong with *L. exigua.*

At the time I described *L. exigua* (1956), I did not have chromosome counts of *L. aurea,* or of *L. exigua* var. *lutea.* The fact that *L. aurea* is a polyploid ($n = 24$) firmly supports the separation of *L. exigua* as a distinct species and permits a more reasonable interpretation of the geography of the two species. As information concerning *L. exigua* has been gradually accumulated, it has become clear that this species is in many respects the evolutionary counterpart of *L. uniflora* but in the eleven paired chromosome series instead of the fifteen paired series. Next to *L. uniflora, L. exigua* has the widest geographic range of any other species. Also, it follows close to *L. uniflora* in not only being self-compatible but in being autogamous as well. The flowers are the smallest in the eleven paired chromosome series and they lack fragrance, two features also characteristic of *L. uniflora.*

PLATE 12. Specimens showing characteristics of plants and some of the variation in a population (5933) of *L. exigua* var. *lutea*.

The isolation and differentiation of populations outside of the Central Basin of Tennessee are an interesting feature of *L. exigua*. The main area of distribution, as shown in Map 2, is made up of a series of populations on appropriate cedar glades that occur in a complex pattern nearly the full length of the Central Basin. About one hundred and fifty miles to the north, with no known stations of *L. exigua* in between, a rather extensive population of plants with certain distinguishing characteristics is to be seen. This area in Bullitt County, Kentucky, is in need of further exploration, for my attempt at field work there in early April, 1962, was under very unfavorable weather conditions. Plants were brought back to the greenhouse where they were grown to maturity and a chromosome count of n = 11 was obtained. Beyond that, the plants were not worked with intensively as was the case with representatives of other populations of the species. This Kentucky population is distinctive on the basis of longer styles, green instead of light lavender sepals and more sharply divided leaves as compared to var. *exigua* and we have named it var. *laciniata.*

To the south of var. *exigua*, isolated by about a hundred miles distance, is var. *lutea* centered in Jefferson County, Alabama. Several populations of this yellow-flowered variety have been studied and they were found to be strongly self-compatible and self pollinating. Here, also the yellow flower color is a fixed feature, not present elsewhere in the species. The populations of var. *exigua* in northwestern Georgia are isolated from the main distributional area of this variety in Tennessee and slight differences in growth habit and other characteristics are noticeable in them. It is evident that *L. exigua* as a whole shows a considerable range of variation, with the most extreme forms isolated at some distance from the main distributional area. Without doubt, the self-compatible and at least facultatively self pollinating breeding system has been important in enabling this diversity to develop.

Some comment should be made concerning a specimen of var. *exigua* in the University of Michigan Herbarium. This specimen is from the private herbarium of Geo. L. Ames, M. D., and was collected in Tennessee in March, 1855. The locality given appears to be Decatur County but the writing is not as clear as one would like it to be. If, as is possible, this specimen did come from Decatur County, the range of var. *exigua* is considerably west of that shown on my map (Map 2). We have not seen any other specimens from west of the Tennessee River and I do not know whether suitable glade sites occur there.

4. **Leavenworthia aurea** Torrey, Ann. Lyc. Nat. Hist. N. Y. 4: 88. 1837

Plate 13

Glabrous winter annual; early leaves with nearly orbicular and entire terminal lobes, later leaves long-petioled, thick, lyrately pinnatifid but usually with only a few lateral lobes, terminal lobe much larger than lateral, lobes entire to shallowly dentate, mature leaves 2-8 cm. long, 1-1.5 cm. wide; early and mid-season flowers scapose, scapes 3-9 cm. long; later flowers usually borne in a raceme on lateral decumbent branches, pedicels relatively thick, 3-6 cm. long; sepals greenish turning light lavender upon drying, non-saccate, narrowly oblong, 4-5 mm. long; petals lemon yellow to orange yellow, changing to light lavender upon drying, narrowly lingulate, very shallowly emarginate, 7-10 mm. long, 3.5-5 mm. wide; anthers of paired stamens introrse; siliques strongly flattened parallel to septum, thickish, erect, 1.5-3 cm. long, 4-5.5 mm. wide, 2-3 mm. thick when fresh; styles 2-3.5 mm. long; gynophore evident, nearly 1 mm. long; seeds 5-11 per silique, dark brown, nearly orbicular, flattened, flat on inner face, low dome-shaped on outer face, narrowly winged, 3.5-4.5 mm. in diameter, areolae of seed-coat reticulum much smaller over embryo than in wing area; radicle of embryo straight; cotyledons nearly orbicular. $n = 24$.

Type in the New York Botanical Garden Herbarium, near Ft. Towson, Oklahoma, *M. C. Leavenworth s.n.* Isotype GH.

DISTRIBUTION: extreme southeastern Oklahoma and in the vicinity of San Augustine, Texas (Map 1). **Oklahoma.** CHOCTAW CO.: 1 mi. west of Ft. Towson, *Rollins 6152* (GH); 9 mi. east of Hugo, *Rollins 5972* (GH); 5 mi. west of Ft. Towson, *G. T. Robbins 2872* (UC); same locality, *McVaugh 7618* (GH, MICH). MC CURTAIN CO.: 4 mi. north of Idabel, *Rollins 5974* (GH); 3.2 mi. west of Idabel, *Rollins and Chambers 5769* (GH); 9 mi. west of Idabel, *Rollins 5973* (GH). **Texas.** Without locality, *M. C. Leavenworth* (NY); 1 mi. east of San Augustine, SAN AUGUSTINE CO., *D. S. and H. B. Correll 23543* (GH, LL); near same locality, *D. S. and H. B. Correll 24817* (GH, LL).

I have deliberately refrained from repeating the specimen citations given in my previous paper (Rollins, 1956) except for the type. The type sheet at the New York Botanical Garden apparently has material collected by Leavenworth both in Texas and near Ft. Towson, Oklahoma, on it, although one cannot be completely certain of this. We do know from Torrey's own words that he received material

Plate 13. Specimens showing characteristics of plants and some of the variation in a population (5771) of *L. aurea.*

collected by Leavenworth from C. W. Short and also direct from Leavenworth. His statement (op. cit.) is as follows, "For my first knowledge of the *L. aurea* I am indebted to my friend Dr. Short of Kentucky, who shared with me the specimens he received from Dr. Leavenworth, its discoverer. Subsequently I received some excellent specimens from Dr. L. himself." It is interesting that Leavenworth managed to collect *Leavenworthia aurea* from the only areas in which it is known to occur today. The Texas location is very restricted in size, being limited so far as we know to San Augustine, where E. J. Palmer collected it in 1915 and again in 1918, and to an area just east of San Augustine where the Corrells made collections in 1961 and 1962. I have searched for the species at San Augustine several times and on the last occasion I found the characteristic wet limestone pavement with *Nostoc*, *Sedum*, and *Opuntia* present, all usual associates of *Leavenworthia* but it was too late in the season to find *L. aurea*. Leavenworth must have collected his Texas specimens at or near San Augustine. It is known from a letter from Leavenworth to Torrey (cf. McVaugh, 1947) that he collected plants at St. (now San) Augustine in Texas on at least one occasion. While stationed at Fort Jesup and nearby Camp Sabine in western Louisiana, Leavenworth traveled into Texas several times.

We had one lot of seed collected by Correll from the Texas locality but we have not had any growing plants because the seed would not germinate. For this reason, our chromosome count for the species is based on collections from southeastern Oklahoma. The fact that this number, n = 24, does not show a strict polyploid relationship to the known counts for other species of *Leavenworthia*, makes it highly desirable to obtain counts from plants of the isolated Texas population. Such information might provide a clue as to the origin of *L. aurea*. As it is, there is only morphological evidence on which to base a suggestion as to its possible relationship. In this respect *L. aurea* is nearest to *L. exigua* var. *lutea* which is the only yellow-flowered population of that species. Var. *lutea*, with thinner siliques, shorter styles and a chromosome count of n = 11, is also highly restricted geographically, being confined to cedar glades in Jefferson County, Alabama.

The thick leaves, rather stout pedicels or scapes and general succulence of *L. aurea* are characteristics often found in polyploids. The relatively high chromosome number of this species is surely the result of polyploidy and it seems quite certain that plants of the *L. exigua* var. *lutea* type entered into the combination that ultimately produced *L. aurea*. Whether another species or some other divergent type of *L. exigua* also figured in that combination is a matter of pure conjecture. Considering *L. aurea* from the standpoint of its present remote geographic position, far to the west of what must have been the center of origin and differentiation of the genus, the question of its route of migration inevitably arises. Two items bear on this question, one the position of the similar *L. exigua* var. *lutea*, itself isolated, south of the main center of *Leavenworthia*, the other the presence of the dissimilar *L. uniflora* extending to the north and west of this center. *L. uniflora* certainly migrated to the Ozarkian glades of Missouri, where it occurs in great abundance, and it seems probable that if *L. aurea* or its direct progenitor spread westward along the same route, some remnant would be there now. However, this is not the case, unless the plant has been completely overlooked. On the other hand, if the progenitor or progenitors of *L. aurea* migrated along a more southerly route, through Alabama, Mississippi and Louisiana, the only suitable habitats known to me remaining today are the glades in Alabama where *L. exigua* var. *lutea* occurs. The development of the Mississippi River embayment region could easily have extinguished any habitats suitable for *Leavenworthia* present in that area at an earlier geological time.

5. **Leavenworthia stylosa** Gray. Bot. Gaz. 5: 26. 1880

Plate 14

Glabrous winter annual; leaves of fully grown plants homomorphic, mostly basal, lyrately pinnatifid, petiolate, 2-10 cm. long, lobes mostly shallowly dentate, sometimes more deeply so, terminal lobe markedly larger than lateral lobes; early season flowers scapose, scapes 3-10 cm. long, later flowers often borne on lateral decumbent branches in loose few- to several-flowered **racemes**; these branches up to 2 dm. long including the pedicels; pedicels 3-7 cm. long; young buds pendant, older buds erect; sepals linear-oblong, non-saccate, 4-8 mm. long, spreading at right angles at full anthesis; petals obovate to broadly spatulate, deeply emarginate, white, yellow or lavender on blade, yellow to orange on claw, usually with a light horizontal band between blade and claw, 9-15 mm. long, 5.9 mm. wide, blade spreading at right angles during full anthesis; stamens strongly tetradynamous, single anthers introrse, paired anthers extrorse; siliques oblong to linear, obtuse above and below, nerveless, fleshy, 1-3 cm. long, 2.5-4.5 mm. wide, 2-4 mm. thick when fresh; gynophores evident, ca. 1 mm. long; styles 3-7 mm. long; seeds dark brown, winged, broadly oblong to suborbicular, 3-4.5 mm. long, 2-3.5 mm. broad, wings thick, less than 0.25 mm. wide, seed-coat shallowly reticulate, cleft with crest at one side of basal end; embryo nearly straight with radicle often slightly bent towards an accumbent position. n = 15.

Type in the Gray Herbarium, cedar barrens at Lavergne, Tenn., June 2, 1879, *A. Gattinger s.n.* Isotypes GH, NY.

DISTRIBUTION: Central Basin of Tennessee (Map 2). BEDFORD CO.: 3 mi. north of Deason, *D. G. Lloyd 350* (GH); wet field along country road leading west from Deason, *Sharp and Sherman 23002* (GH); 3 mi. south of Unionville, *Rollins 5534* (GH, US). DAVIDSON CO.: 1.5 mi. east of Una, *Rollins 6137* (GH); 2 mi. northeast of Lavergne, *Rollins 55161* (GH, US); near Mt. View school, *Svenson 10237* (GH); cedar barrens south of Nashville, *Sharp and Shanks 381* (GA, GH, MICH, TENN); near Hurricane Creek, about 3 mi. northeast of Lavergne, *Rollins 59105* (GH). RUTHERFORD CO.: 4 mi. east of Lascassas, *Rollins 5902* (GH); near Murfreesboro, *E. J. Palmer 35487* (GH); 1 mi. east of Eagleville, *Rollins 61167* (GH); south of Murfreesboro, *Shanks and Sharp 386* (GH); 13 mi. southeast of Murfreesboro, *Rollins and Channell 5652* (GH); 5 mi. southeast of Kirkland, *Rollins 5523* (GH, US); 1.5 mi. northeast of Readyville, *Rollins and De Selm 55123* (GH, US); 3 mi. northwest of Murfreesboro, *Rollins, Solbrig, Hilferty and Lloyd 6030* (GH); 4.5 mi. northeast of Stewart Air Base, extreme northeastern Rutherford County, *Rollins 6142* (GH); 2 mi. north of Walterhill, *Rollins and Chambers 5739* (GH). SMITH CO.: west of Carthage, *Sharp and Sherman 22740* (GH). WILSON CO.: 5.8 mi. west of Gladeville, *Rollins and Chambers 5750* (GH); 2 mi. north of Lebanon, *R. C. and D. Rollins 5206* (GH); Vesta, *Svenson 7750* (GH); 10 mi. south of Hartsville, *Rollins 5303* (GH, US); 3 mi. west of Lebanon, *Rollins and Bold 55140* (GH, US); 3 mi. west of Norene, *Rollins and Channell 5913* (GH); 10 mi. south of Lebanon, *Rollins, Solbrig, Hilferty and Lloyd 6009* (GH).

The type material of *L. stylosa* is yellow-flowered and the species was so described by Gray. It is true that exclusively yellow-flowered populations occur near Lavergne where Gattinger first collected the species. Extending north and east there is an extensive area in southeastern Davidson County and in adjacent Rutherford and Wilson Counties where hundreds of thousands of yellow-flowered plants make up the populations. Features correlated with the yellow-flowered plants of that area are a fleshy short fruit and a relatively long style (cf. Table 4). There are also exclusively yel-

PLATE 14. Specimens showing characteristics of plants and some of the variation in a population (5746) of *L. stylosa*.

low-flowered populations in the vicinity of Lebanon, Wilson County, but these plants have elongated fruits much like those of white to lavender-flowered plants of the same general area. Over much of the eastern part of the range of *L. stylosa*, the populations are made up of predominantly white or lavender-flowered plants. The observation made by Baldwin (1945, p. 371) that "yellow is much the commonest color," in *L. stylosa* does not hold. Actually, off-white to light lavender is the most frequent flower-color, considering the species as a whole. It is interesting that in many populations there is a wide range of intensity of the lavender color from plant to plant. There is less of a range of intensity of the yellow color in yellow-flowered populations.

Frequently seen are one or a few yellow-flowered plants among thousands of white-flowered individuals as well as the reverse situation with sporadic white- or lavender-flowered plants showing up among thousands of yellow-flowered individuals. My assumption from field observations alone is that these are mutant forms that arise here and there in the populations of which they are a part. The result of this easy mutational switch from one flower-color to another is extensively seen in the northeastern, eastern and southern parts of the range of *L. stylosa* but I have never seen evidence of it in the exclusively yellow-flowered populations of southeastern Davidson County and the area immediately adjacent.

What is apparently a different kind of admixture of yellow- and white-flowered plants occurs west of Gladeville in Wilson County. In this area, there is a gradual transition from predominantly white- to lavender-flowered populations in the area around Gladeville to predominantly yellow-flowered populations about six miles to the west. In this distance, it appears that a gradual intermixing of the two major color forms is actively taking place.

From field observations and from careful examination of greenhouse and garden materials, it is clearly evident that *L. stylosa* is indeed a highly variable species as Baldwin (l. c.) has pointed out. The question as to whether this variation is at random throughout the species or whether there are correlations of characteristics and/or local geographic areas was not commented on by him. As we see it, the variation present is not at random. There appear to be three areas within the total range of the species which reflect separate trends within its overall variation pattern. It is suggested that these areas coincide with extensive glade systems, probably somewhat separated from each other for a considerable period of time, which allowed the evolutionary development of recognizable morphological types.

The glade system centering in southeastern Davidson County and bounded on the east by Stones River has exclusively yellow-flowered populations. Correlated features are relatively short, thick fruits with long styles. In the Murfreesboro area, particularly to the east, south and southwest, a white to light-lavender flowered form is correlated with relatively long, narrow and somewhat torulose fruits with shorter styles. Again, the assumption is that these features developed in a glade system long isolated from the Davidson County series. A third distinctive development in *L. stylosa* seems to have centered in Wilson County from the Cedars of Lebanon State Park northward. Flower color is not a distinguishing feature here because both white and yellow flowered types occur. However, the fruits are somewhat intermediate between the Davidson County and the Murfreesboro types, being neither as long as the latter nor as short and fleshy as the former.

6. **Leavenworthia torulosa** Gray. Bot. Gaz. 5:26. 1880

Plate 4, fig. 4 & 5

Glabrous winter annual; early leaves usually entire with a remote cordate lobe, leaves of fully grown plants lyrately pinnatifid (2-) 3-8 (-9) cm. long, lobes nearly entire to shallowly and broadly dentate, sometimes more deeply lobed, terminal lobes markedly larger than lateral lobes; early and mid-season flowers scapose, scapes 3-8 (-10) cm. long, later flowers often borne on lateral decumbent branches in loose few to several flowered racemes, these branches up to 2 dm. long including pedicels; fruiting pedicels 3-7 cm. long, straight or gently curved upward; young buds pendant, older buds erect; sepals nonsaccate, light lavender to slightly greenish, divergent to nearly erect during full anthesis, narrowly oblong, 3.5-5.5 mm. long; petals emarginate, spatulate, 6-10 mm. long, 3.5-6 mm. wide., white to light lavender, occasionally deep lavender or yellow; siliques linear, strongly torulose even when young, 1.5-3 cm. long, 2.5-4 mm. wide, 2-3.5 mm. thick when fresh; styles 2.5-5 mm long; gynophore evident, ca. 1 mm. long; seed nearly wingless, longer than broad, 2.5-3.5 mm. long, areolae of seed-coat reticulum nearly uniform in size throughout; radicle of embryo slightly bent. n = 15.

Type in the Gray Herbarium, collected in the "barrens of Kentucky" by *C. W. Short*, 1840. **Isotypes** GH, NY.

DISTRIBUTION: southern Kentucky to southern Tennessee (Map 1). **Kentucky.** "on wet rocks in the west of Kentucky," *C. W. Short 1837* (GH); cedar glade situation, 12 mi. north of U. S. Highway 68 on state route 1083, Warren County, April 1, 1959, *R. C. Rollins and R. B. Channell 5906* (GH, VDB). **Tennessee.** BEDFORD CO.: 1 mi. south of Unionville, *Rollins 5533* (GH, US); 6 mi. southeast of Eagleville, *Rollins and Chambers 5734* (GH); 1 mi. southeast of El Bethel, *Rollins 59101* (GH). BRADLEY CO.: in small cedar barren east of Cleveland, *Sharp, Felix and Adams 10566* (GH, UT); 1.5 mi. east of Cleveland, *Rollins 5901; 5998; Rollins and Chambers 5701* (GH). DAVIDSON CO.: 1 mi. west of Bordeaux, *R. C. and D. Rollins 5210* (GA, GH, US); wet limestone flats about Nashville, March 19, 1880, *Gattinger s.n.* (GH); 1.5 mi. east of Una, *Rollins 6138* (GH); near Mill Creek, 14 mi. south of Nashville, *Rollins and Channell 5620* (GH). GILES CO.: 3.5 mi. southwest of Pulaski, *Rollins and Chambers 5723* (GH); 4 mi. south of Aspen Hill, *Rollins and Channell 5627* (GH). LINCOLN CO.: southeast of Fayetteville, *Sharp, Felix and Adams 10884* (GH); west of Harms, *Sharp, Felix and Adams 10851* (GH). MARSHALL CO.: 4 mi. southwest of Cornersville, *Rollins and Channell 5626* (GH); 5 mi. north of Lewisburg, *Rollins 5922* (GH); 2 mi. south of Chapel Hill, *Rollins and Chambers 5728; 57142* (GH); 1 mi. north of Chapel Hill, *Rollins and Chambers 5732* (GH). MAURY CO.: 5 mi. west of Columbia, *Rollins 55109* (GH); 6 mi. north of Culleoka, *Sharp, Felix and Adams 11134* (GH); Rally Hill, *Rollins 5920* (GH). RUTHERFORD CO.: 2 mi. south of Eagleville, *Rollins 5531* (GH, US); Stones River Military Park, *Sharp, and Shanks 452* (GA, GH, MICH, US); 2 mi. south of Lavergne, *Rollins and Chambers 5741* (GH); 4 mi. southwest of Murfreesboro, *Rollins and Channell 5656* (GH); 1 mi. east of Eagleville, *Rollins 61166* (GH). SUMNER CO.: 4 mi. east of Gallatin, *Ralph M. Kriebel 9373* (PUL); Gallatin, *Deam 61330* (MICH). WILLIAMSON CO.: Kirkland, *Rollins 53144; 55113* (GH); 1 mi. north of College Grove, *R. C. and D. Rollins 5215a* (GH); 1 mi. north of Nolensville, *Rollins 6150* (GH). WILSON CO.: 4 mi. southwest of Lebanon, *Rollins and Chambers 5752* (GH); 3 mi. northwest of Gladeville, *D. G. Lloyd 385* (GH); 2 mi. north of Green Hill, *Rollins 5311* (GH); 12 mi. west of Lebanon, *Rollins and Channell 5908* (GH).

Unlike *Leavenworthia stylosa*, all populations of *L. torulosa* so far tested have been found to be self-compatible. In the greenhouse, without any manipulation of the flowers, self-pollination will only rarely take place. However, the plants are highly self-compatible and it takes only a weak pinch of the flower between the forefinger and thumb to bring about adequate pollination resulting in full seed set. Insect visitation to the flowers under natural conditions is frequent and it is likely that a complex mixture of outcrossing and selfing occurs in any given population.

The stance of the flower parts is very much affected by the brightness or dullness of the day. On bright days, the sepals are widely spreading and the limb of each petal is rigidly bent at right angles to the erect claw, providing a maximum target for a flying insect. On dull, overcast days, the sepals and petals remain nearly erect, spreading only slightly from a closed position. On such overcast days, which are usually quite cool during the flowering season of *Leavenworthia,* insect activity is at a minimum, if it is not wholly absent. Under these conditions, autogamy takes place following self-pollination. The position of the sepals and petals is such that the anthers are guided into the stigma as the filaments elongate. In the species as a whole, it appears that both selfing and outcrossing are importantly involved in the breeding system.

Flower color in *L. torulosa* ranges from white to deep lavender with the center of the flower being predominantly yellow. In some flowers the center tends in the direction of orange. The most prevalent color of the outer petals is light lavender on either the upper or the lower surface with white on the opposite surface. In some populations the upper petal surfaces are predominantly white with the lower surfaces light lavender. In other populations the upper surfaces are light lavender with the lower surfaces white. Yellow as a color of the petal blade is very rare in *L. torulosa.* In fact out of over a hundred populations examined, only one had a few yellow-flowered plants in one spot. Quite in contrast to the flower-color situation in *L. stylosa,* where yellow, white, light lavender and deep lavender occur in many combinations in a very complex way, yellow as a flower color is essentially absent in *L. torulosa.*

There is considerable variation in *L. torulosa* on a species-wide basis but the range of variation is not as great as that found in *L. stylosa.* This can be seen by comparing the measurement data on flowers and fruits of the two species in Tables 3 and 4, but it is also noticeable in the field, particularly when the range of variation within individual populations of each species is compared. The flowers of some populations of *L. torulosa* are distinctly sweet-scented; in other populations the odor is faint; in still others, there is no detectable odor. My impression is that the odorless populations are most apt to be peripheral to the main range of the species but this point needs to be systematically checked. From the study of collected specimens and from field observations it is evident that the peripheral populations (e. g., Warren Co., Kentucky; Bradley Co., Tennessee) are also the most divergent morphologically from the populations near the distributional center of the species.

The geographical range of *L. torulosa* is somewhat greater than that given by Baldwin (1945) but I agree with him that there is no solid evidence in support of its occurrence in Louisiana, Missouri or Arkansas, as single questionable specimens in herbaria might suggest. The center of development is undoubtedly in the Central Basin of Tennessee. In Kentucky, we found it in only one place and the population is very limited in size. I searched for the species in Kentucky in three different years before finding it and I have not seen any specimens from that state collected in the interim between those of Short in the 1840's and the small population we found in 1959. At the southern extremity of its range, the species is abundant in a cedar glade in Giles County, Tennessee, only a few miles north of the Alabama line. The most southeasterly population, in Bradley County, only a few miles north of the Georgia line, is relatively small by comparison with populations in the Central Basin of Tennessee and the plants resemble those of Kentucky in a number of features.

Baldwin (l. c., p. 370) suggested that *L. torulosa* apparently intergrades with *L. stylosa* but I have seen no convincing evidence that it does. We have not been able to obtain hybrids between these two species, even though they have the same chromosome number, and I find that the seeds of *L. torulosa* are sharply distinct from those of *L. stylosa*, in addition to the other character differences that are usually emphasized. The flowers of *L. torulosa* are always much smaller than those of *L. stylosa* (cf. Table 3). In fruit, the torulose siliques, shorter styles and wingless seeds satisfactorily characterize *L. torulosa*. There is a slight tendency towards torulosity of fruits in some populations of *L. stylosa* and this may have been the source of some confusion in the past.

7. **Leavenworthia uniflora** (Michx.) Britton, Mem. Torrey Club 5:171. 1894

Plate 15

Based on *Cardamine uniflora* Michx., Fl. Bor.-Am. 2:29. 1803. Type at P; photo of type at GH.

Leavenworthia Michauxii Torrey, Ann. Lyc. Nat. Hist. N.Y. 4:89. 1837. Based on the same type as *Cardamine uniflora* Michx.

Glabrous winter annual; early leaves with a single remote terminal dentate lobe, later leaves deeply pinnatifid with up to 9 pairs of subequal acutely dentate lobes, gradually increasing in size from petiole towards apex, terminal lobe only slightly larger than adjacent pair, leaves 2-10 cm. long, 5-10 mm. wide, forming a rosette during first portion of plant growth; flowers mostly scapose, true stems with loose racemes of flowers formed only under favorable growing conditions and late in the particular plant growth cycle; sepals non-saccate, oblong, greenish at first, purplish later or upon drying, 3.5-5 mm. long; petals white, narrowly lingulate, truncate, usually erect, 5-7 mm. long, 2.5-3.5 mm. wide; anthers of paired stamens introrse, small; siliques thick and fleshy, erect, 1.5-3 cm. long, 3-5 mm. wide, 2.5-4 mm. thick when fresh; styles 1.5-3 mm. long; gynophore evident, ca. 1 mm. long; seeds dark brown, widely wing-margined, nearly orbicular, flattened, 3-4 mm. in diameter; areolae of seed-coat reticulum smaller over embryo than in wing area; radicle of embryo loosely adpressed along margin of cotyledons, approaching the accumbent position but scarcely accumbent; cotyledons nearly orbicular. $n = 15$.

DISTRIBUTION: northern Alabama and northwestern Georgia to southwestern Ohio and west to southern Missouri and northwestern Arkansas. **Alabama.** JACKSON CO.: 5 mi. west of Scottsboro, *Rollins 55196* (GH); Larkinsville, *Rollins and Channell 5649* (GH). LAWRENCE CO.: 1.5 mi. west of Wren, *Rollins 5982* (GH); 8 mi. east of Wren, *Rollins and Chambers 5718, 57138* (GH); 3 mi. east of Speake, *Lloyd 258* (GH); 5 mi. southwest of Danville, *Rollins 6126* (GH). MADISON CO.: Smither's Mt., *Harper 3555* (GH, US); southwest slope of Monte Sano, near Huntsville, *Rollins and Channell 5648* (GH). MORGAN CO.: near Danville, *Rollins 55190* (GH, US); 4 mi. southwest of Lebanon, *Rollins 6113* (GH); 2 mi. south of McKendry, *Rollins 6123* (GH); 5 mi. southwest of Massey, *Lloyd 264* (GH); 1/2 mi. west of Falkville, *Rollins and Chambers 5709* (GH); about 2 mi. south of Falkville, *Lloyd 680* (GH). **Tennessee.** BEDFORD CO.: 6 mi. south of Eagleville, *Rollins and Channell 5660* (GH); 1 mi. east of El Bethel, *Rollins 5999* (GH); southwest of Ray Chapel, *Sharp, Felix and Adams 11160* (GH). KNOX CO.: Knoxville, *Ruth 358* (GH, MICH); Sequoia Hills, Knoxville, *Drew et al 413* (GA). MARSHALL CO.: 1 mi. north of Chapel Hill, *Rollins and Chambers 5733, Rollins 5317* (GH); 1.5 mi. south of Lewisburg, *Rollins and Chambers 5726* (GH). MAURY CO.: 2 mi. north of Rally Hill, *Rollins 5917* (GH); 21 mi. north of Lewisburg, *Rollins and Channell 5622* (GH); east of Columbia, *Sharp, Felix and Adams 11084* (GH). RUTHERFORD CO.: 4 mi. east of Lascassas, *Rollins 5903* (GH); 2 mi. south of Lavergne, *Rollins and Chambers 5740* (GH); 13 mi. southeast of Murfreesboro, *Rollins and Channell 5651* (GH); northeast of Lavergne, *Sharp and Shanks 380* (GA, GH, MICH, TENN, US); 1.5 mi. north of Eagleville, *R. C. and D. Rollins 5220* (GA, GH). WILSON CO.: 3 mi. east of Lebanon, *Rollins, Solbrig, Hilferty and Lloyd 6003* (GH); south of Lebanon State Park, *Sharp and Sherman 22741a* (GH). **Georgia.** WALKER CO.: 5.5 mi. south of Chickamauga, *Pyron and McVaugh 2701* (GA). **Ohio.** ADAMS CO.: Mineral Springs region, May 2, 1932, *E. L. Brown s.n.* (OS); Lynx, April 2, 1938, *Floyd Chapman s.n.* (OS). HIGHLAND CO.: Brush Township, *Bartley and Pontius 589* (NY, OS, US); PIKE CO.: Sunfish Creek near Byton, June 7, 1931, *Bartley and Pontius s.n.* (OS). **Indiana.** CLARK CO.: along Lick Creek, 1 mi. east of Charleston, *Deam 24531* (GH); Charleston, 1877, *C. R. Barnes s.n.* (GH, PUL, US); same locality, 1878, *J. M. Coulter s.n.* (GH). **Kentucky.** Barrens of western Kentucky (probably near Bowling Green) *C. W. Short s.n.* (GH, NY, US). BARREN CO.: Glasgow Junction, "sinkhole" northwest of town, *John Hussey s.n.* (PUL). CALDWELL CO.: Princeton, *A. M. Harvill* (*Baldwin 2551*, MICH). CHRISTIAN CO.: 2-3 mi. west of Hopkinsville, *Hardin 378* (GH, MICH, US). LOGAN CO.: 3 mi. southwest of Russellville, *Rollins and Channell 5905* (GH). SHELBY CO.: Shelbyville, *M. B. Flint s.n.* (GH). SIMPSON CO.: near Tenn. line, *Baldwin 2554* (MICH). **Arkansas.** BENTON CO.: near Eureka Springs, *Canby 7* (GH); same locality, *B. F. Bush 1531* (GH, US). CARROLL CO.: near Elk Ranch, *Palmer 29828* (NY). **Missouri.** CHRISTIAN CO.: near Bull Creek, *Rollins 61160* (GH). DALLAS CO.: barrens, *Canby 8* (GH). FRANKLIN CO.: Gray Summit, *M. Ownbey 1179* (GH). JEFFERSON CO.: 1887, *H. Eggert s.n.* (GH, US). LACLEDE CO.: near Hazel Greene, *Steyermark 8500* (US). MADISON CO.: mine La Motte, *Palmer 39183* (GH). OZARK CO.: 10 mi. west of Theodosia, *Rollins 61163* (GH). ST. LOUIS CO.: 1883, *G. W. Letterman s.n.* (GH, US). TANEY CO.: 6 mi. west of Forsyth, *Rollins 61161* (GH); 7 mi. west of Rueter, *Rollins 61162* (GH).

In areas where *Leavenworthia uniflora* occurs with other species of the genus, it is earliest to flower. In some seasons it is as much as two or three weeks ahead of the others (cf. Table 6). This is undoubtedly of significance because *L. uniflora* approaches being fully autogamous and may be wholly so under some circumstances. Thus, as a species it may exist wholly independent of insect pollination and is not at all limited as to earliness of flowering by the lack of insect vectors. On the assumption that selection pressure has operated to favor earliness because of the preadaptation of all species of *Leavenworthia* to wet or at least moist situations which are most likely in very early spring, *L. uniflora* has distinct advantages over the less fully autogamous species and particularly over those that are self-incompatible. The comparatively wide geographical distribution of *L. uniflora* appears to be attributable to the development of auto-

PLATE 15. Specimens showing characteristics of plants and some of the variation in a Tennessee population (5622) of *L. uniflora*.

gamy allowing distant single-seed dispersal along with the species concomitant emancipation from dependence on insect pollination and its increased seed production over that of other species.

The flowers of *L. uniflora* are the smallest in the genus and the petals are always white on the blade, tending towards a light yellowish green on the claw. It is difficult to understand the early confusion of Torrey (1837) in particular, and to some extent that of Gray (1880), as to flower color, because even upon drying the whiteness of the petals is retained. However, both were working from fragmentary material as shown by their preserved specimens in the New York Botanical Garden and the Gray Herbarium. In most of the populations I have observed, the petals tend to be nearly erect or at least ascending even when there is ample sunshine and the other nearby species of *Leavenworthia* have the limb of the petals expanded to a position at right angles to the claw. In this respect, *L. aurea* and *L. uniflora* are most alike. It is evident that there is variation of limb position in *L. uniflora* and in different populations the extent of flower opening is different. Pictures of plants of a Missouri population show the petals widely extended. It should be re-emphasized that flower expansion in all species of *Leavenworthia* is very strongly influenced by light intensity. The flowers will close in less than an hour if the sky becomes cloudy following a sunny period. In the self-compatible species, such as *L. uniflora*, where the anthers are introrse, the closing of the flower insures self-pollination. The anthers of *L. uniflora* are relatively small and under ordinary conditions are often in direct contact with the rather broad stigma.

The siliques of *L. uniflora* are characteristically thick and the valves are smooth. The style is relatively short but the length differs significantly in different populations. Both the thickness, which is due to a fleshiness of the valve walls, and the style length are altered when specimens are dried. The styles are always longer in dried than in fresh material because of the contraction of tissue at and below the base of the style. Also, the siliques are less thick on prepared specimens than on live plants because the fleshiness is completely lost. As with other species of the genus, the length of the siliques may be strongly influenced by the size and vigor of the plant. Plants growing in especially favorable sites produce large numbers of relatively long fruits.

The tendency towards scapose flowers is more strongly expressed in this species than in any of the others. Many populations are made up wholly of plants with scapose flowers. However, under very favorable conditions of growth, and late in the growth cycle of the plant, it will produce true branches with racemes of flowers. At present, we do not know what the factor or factors are that cause a shift from the one condition to the other. It is probable that the racemose inflorescence is the more primitive since this type of inflorescence characterizes the *Cruciferae* as a whole.

Leavenworthia uniflora is obviously the most successful species of the genus from the point of view of area occupied (see Map 1). It has also become more successfully adapted to a wider range of moisture conditions, particularly towards the dry side, than any of the other species. This may help to account for its broader distribution. We have found *L. uniflora* in several glades that, although moist or even wet at times, are too well drained to permit standing water, as is characteristic of most of the glades where other species of *Leavenworthia* grow. *L. uniflora* readily invades old fields in areas where cultivated lands extend into, or displace the pre-agricultural glade sites. These fields are often very wet, poorly drained, with a high retained moisture content and stand idle long after better drained farmlands of the area are being actively worked.

From the evolutionary viewpoint, the evidence points to *L. uniflora* as the most highly evolved of the 15-paired chromosome group of species. The self-compatible breeding system, tending towards autogamy, small flower size, introrse anther position, ascending petal stance, fixed petal color, lack of fragrance and tendency towards scapose inflorescence type, are all derived features when assessed in terms of those possessed by *L. stylosa*. As indicated above where breeding systems are discussed, self-incompatibility most frequently precedes self-compatibility and heterogamy precedes autogamy. *L. stylosa* is self-incompatible and therefore obligately heterogamous and insect pollinated. It has relatively large flowers, the anther position is extrorse, the petals are sharply spreading, the petal color ranges from white with yellow claw through yellow with orange claw to lavender with orange claw. The flowers are heavily fragrant and there is a strong tendency towards racemose inflorescences on older plants. Thus, the more primitive conditions, mostly associated with insect pollination, are found in *L. stylosa* while in comparable characteristics, the derived condition is found in *L. uniflora*. The changes could have come about in association with selection pressures favoring a shift from the interdependence of obligate heterogamy and insect pollination towards autogamy and emancipation from the necessity of insect transfer of pollen.

Individual populations of *L. uniflora* are usually relatively uniform except for size and the features associated with size that may be strongly influenced by uneveness in the habitat or the progression of a particular season in relation to the habitat. Even the species as a whole is quite uniform but there are definite differences between populations. This is shown in Table 4, which gives differences in silique dimensions.

I agree with Baldwin (l. c.) that *L. uniflora* is the most distinctive of the species of *Leavenworthia*. It is readily distinguishable from the other species because of the small entire petals and highly dissected leaves. The position of the short radicle, adpressed to the edges of the cotyledons of the embryo, is closer to what is usually found in the *Cruciferae* than is the straight or only slightly bent radicle found in other species of the genus.

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THE TAXONOMY AND DISTRIBUTION OF THE ZYGOPHYLLACEAE OF BAJA CALIFORNIA, MEXICO

DUNCAN M. PORTER

Although the Zygophyllaceae is a rather small family, it contains many important desert plants. The arid Mexican region of Baja California is an excellent area in which to consider the family, as contained within this region are probably more taxa of Zygophyllaceae than in any other area of comparable size in the world. The purpose of this study, therefore, has been to ascertain the taxonomic and geographic limits of the family within Baja California. This has been accomplished through herbarium research, a review of the pertinent literature, and field observations. Collections were made in Baja California from January through March, 1960, while I served in the capacity of Field Biologist for the California Academy of Sciences, San Francisco. This trip was supported financially by a grant from the Belvedere Scientific Fund of San Francisco. The assistance of both institutions is gratefully acknowledged.

The first set of plants from these collections is deposited in the Dudley Herbarium of Stanford University (DS).[1] Duplicate sets are deposited in the Herbarium of the California Academy of Sciences (CAS); Herbario Nacional del Instituto de Biología de la Universidad Nacional de México (MEXU); Conservatoire et Jardin Botaniques, Geneva (G); Herbarium of the University of California, Berkeley (UC); Herbarium of the University of Arizona, Tucson (ARIZ); Herbarium of the University of Texas, Austin (TEX); and the United States National Museum, Smithsonian Institution (US).

This investigation was accomplished under the helpful guidance of Dr. Ira L. Wiggins, former Director of the Natural History Museum, Stanford University. My gratitude is extended to Dr. Wiggins, to the staff of the Dudley Herbarium, and to the herbarium curators, both those in whose herbaria I have had the pleasure of working, and those who have courteously loaned material to be examined,

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[1] The herbarium abbreviations given here and throughout the remainder of the paper refer to those listed by Lanjouw and Stafleu (1959).

for the assistance offered during the investigation. Special thanks are due Dr. Robert C. Foster of the Gray Herbarium, Harvard University, who generously supplied the Latin description for the new species of *Fagonia*, and to Dr. Reid V. Moran of the San Diego Museum of Natural History, who provided cytological material of *Fagonia*.

NOTES ON THE GEOGRAPHY, CLIMATE, AND VEGETATION OF BAJA CALIFORNIA

Baja California is a rugged mass of mountains and arroyo-dissected mesas, with extensive flat, sandy plains in the northeast and along a large part of its Pacific Coast. The highest mountains are found in the north, where the Sierra Juárez and the Sierra San Pedro Mártir, southern extensions of the Laguna Mountains of California, extend along the center of the peninsula from the International Boundary to a latitude of approximately 30° N. The tallest of these peaks, El Picacho del Diablo, reaches a height of just over 10,000 feet. The next highest range is encountered in the Sierra Victoria and the Sierra Laguna of the Cape Region at the southern end of the peninsula, which reach a height of nearly 7,000 feet. The area between the southern end of the Sierra San Pedro Mártir and the northern end of the Cape Region is composed of a series of low, rugged ranges for the most part paralleling, and in close proximity to, the eastern shore of the peninsula. Along the eastern side of these ranges there is a tremendous fault scarp that crosses over to the Pacific Coast just north of the Cape Region. This escarpment is strongly marked in the north and south, but it is not so pronounced in the center of the peninsula. The Sierra Juárez and Sierra San Pedro Mártir rise abruptly out of the San Felipe Desert and slope gradually to the westward. North of the Cape Region, the Sierra Giganta arises abruptly out of the Gulf of California and slopes gently westward to the wide Magdalena Plain, which fronts on the Pacific Coast. To the north, a series of rugged mountains extending completely across the peninsula separates the Magdalena Plain from the Vizcaíno Desert, the largest expanse of flat land on the peninsula, which also faces on the Pacific. Another series of low ranges separates the Vizcaíno Desert from the southern end of the Sierra San Pedro Mártir.

The peninsula is visited in the north by winter rains that may fall from December to March and in the south by summer rains occurring from July to September, with dry periods in between. These wet seasons may overlap to some extent in central Baja California, but they are less likely to occur here with as much regularity as in the extreme north or south. Both rainfall and temperature data for Baja California are meager and cover such short periods that generalizations cannot be based upon them. It is known, however, that temperatures of 90° F and above may be encountered in any month at certain localities, and that other areas have gone as long as seven years without rain.

There are three distinct phytogeographic areas in Baja California (Wiggins, 1960): the Californian, the Cape Region, and the Central Desert (Fig. 1). The Californian flora occupies the mountains and foothills west of the San Felipe Desert to the Pacific Ocean. It extends from the International Boundary to the southern end of the Sierra San Pedro Mártir and is essentially a southward extension of the Southern California flora. The Cape Region flora occupies the Sierra Giganta and most of the region south of La Paz. This flora is most closely allied with the subtropical vegetation to the southeast on the Mexican mainland. The Central Desert flora is found in the more arid region between the first two areas. It also occurs to the east of the Californian flora in the north and in two isolated spots in the Cape Region. This desert flora occupies the western part of the Sonoran Desert, which continues northward into California and eastward into Arizona and Sonora.

The Central Desert flora has been further divided into four subregions (Shreve, 1951). In the northeast, the Lower Colorado Valley lies in the rain shadow of the Sierra Juárez and the Sierra San Pedro Mártir, extending from the International Boundary to Bahía de los Angeles. The Central Gulf Coast continues southward from Bahía de los Angeles. It lies along the eastern side of the drainage divide of the peninsula, continuing with few interruptions to San José del Cabo. The many barren islands in the Gulf of California fall within this subdivision. South of the Californian flora and west of the peninsular divide is the Vizcaíno Region. This region stretches along the Pacific Coast to Punta Pe-

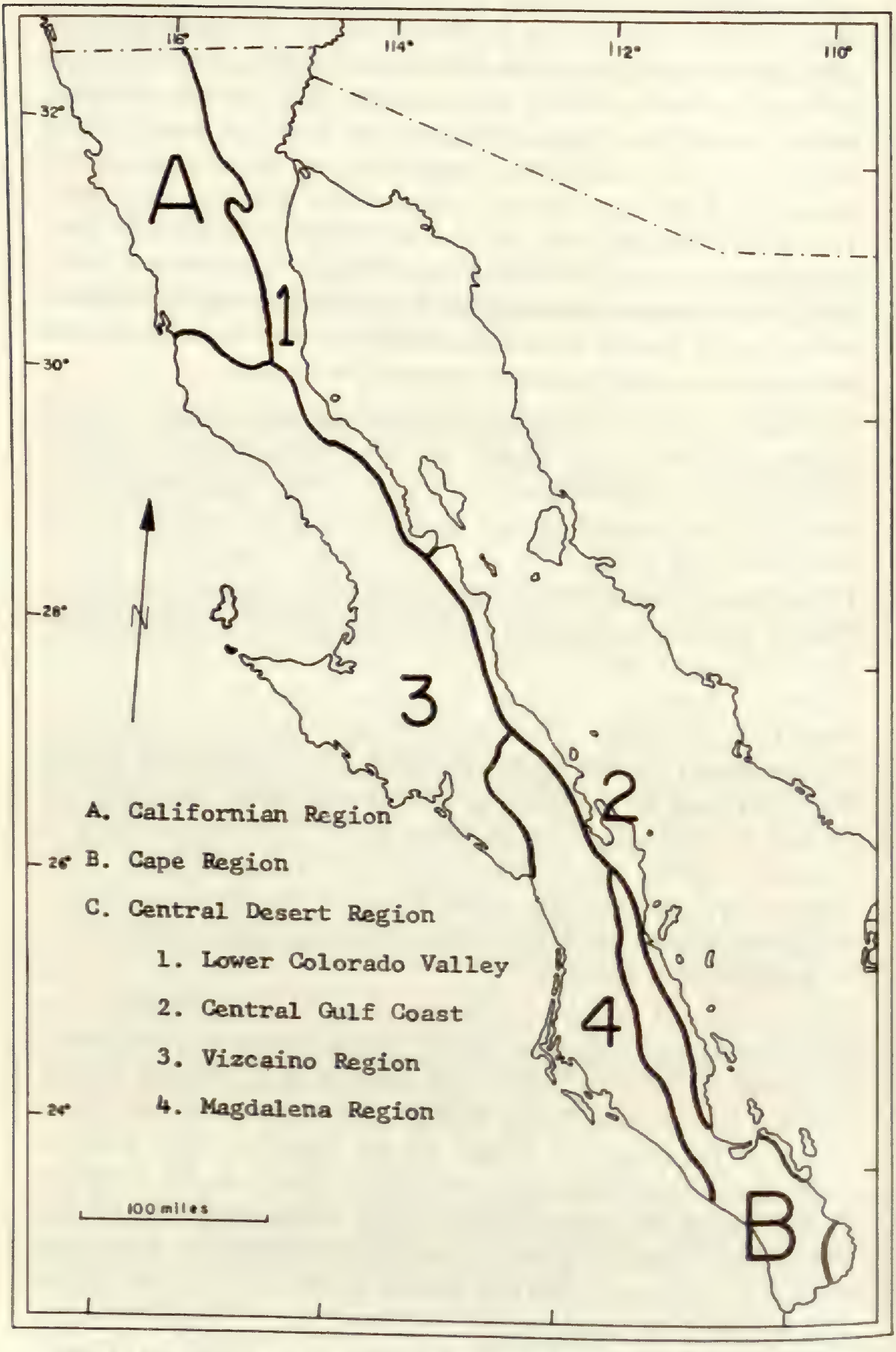

Fig. 1. Map showing the phytogeographic regions of Baja California.

queña, where it is replaced by the Magdalena Region. The Magdalena Region continues west of the drainage divide and the Sierra Giganta to the Cape Region, where it in turn is replaced by the more mesic Cape Region flora.

The plants dealt with in this study are essentially members of the Central Desert flora, although several are found within the Cape Region flora, and at least one is reported to occur in the Californian flora.

There is a wealth of literature available pertaining to the vegetation and flora of Baja California. The following references deal with the more general aspects of the vegetation: T. S. Brandegee (1891), Goldman (1916), Johnson (1958), Johnston (1924), Shreve (1926, 1936, 1937, 1951), and Wiggins (1960).

TAXONOMIC TREATMENT

The Zygophyllaceae is a family of about 25 genera and 250 species, found mainly in the arid tropics and subtropics of both Old and New Worlds. The family is represented in Baja California by 6 genera, 15 species, and 4 varieties.

The order in which the taxa involved are discussed is strictly a matter of convenience, following the order in which they fall in the artificial keys. Phylogenetic lines of development have not been investigated, as the present study is exploratory and preliminary to more searching cytotaxonomic investigations.

Generic descriptions, with the exception of *Guaiacum* and *Larrea*, apply only to those species represented in Baja California.

KEY TO GENERA

Upright divaricate woody shrubs
  Leaves alternate, entire or odd-pinnate; flowers white, drying to yellow, crepe-like .... 1. VISCAINOA.
  Leaves opposite, even-pinnate; flowers blue or yellow, blades of the petals twisted like a propeller
    Flowers blue; leaves of two free leaflets subsessile on the petiole; stipules caducous; filaments not appendaged; capsule tomentose .... 2. GUAIACUM.
    Flowers bright yellow; leaves of two leaflets connate at the base; stipules persistent; filaments appendaged at the base: capsule pilose .... 3. LARREA.
Annual or perennial prostrate to upright herbs or suffrutescent subshrubs

Flowers red-purple; leaves digitately 3-7-foliolate; fruit a glutinous 5-lobed loculicidally dehiscent capsule .... 4. FAGONIA.

Flowers yellow or orange; leaves odd-pinnate; fruit dividing into 5-12 indehiscent nutlets

  Nutlets spiney, 3-5-seeded, as many as the petals; beak of the fruit falling with the nutlets; branches prostrate to upright .... 5. TRIBULUS.

  Nutlets tuberculate, 1-seeded, twice as many as the petals; beak of the fruit persisting after the nutlets fall; branches decumbent .... 6. KALLSTROEMIA.

1. **Viscainoa** Greene, Pittonia 1:163. 1888

Divaricately-branched leafy shrubs 2-3(-6) m. high, branches crooked at the nodes; younger branches green, tomentose; bark on older branches gray, glabrate except at the nodes; flowering branches few-many-flowered, leaves crowded; herbage usually canescent (younger parts especially so), tomentose to lanate. Stipules subulate to linear-lanceolate, 2-13 mm. long, caducous. Leaves alternate, entire or odd-pinnate with 3-5 leaflets. Flowers 2-3 cm. in diameter; peduncles 1-several-flowered, opposite the leaves, to ca. 2 cm. long; pedicels reflexed, tomentose, 6-20 mm. long. Sepals 4-6, free, tomentose (pilose at base of inner surface), obovate to elliptic, apex obtuse to acute, deciduous. Petals 4-6, white, crepe-like, yellowing with age, obovate, short-clawed, strongly veined. Stamens 8-12, twice the number of the petals, inserted on the inconspicuous disc; filaments subulate to dilated at the base; anthers sub-basifixed, sagittate, 2-4 mm. long. Ovary 3-5-lobed, 3-5-loculed, pilose, on a short gynophore ca. 1 mm. long; ovules 2 per locule, placentation axile; style ca. 2 mm. long, persisting to form a beak on the fruit; stigma with as many lobes as locules in the ovary. Fruit an inflated, 3-5-lobed, 3-5-loculed, tomentose, slightly reticulate, coriaceous, obovoid, septicidal capsule; cinereous to green, drying to tan; carpels separating at maturity and splitting along the placentae, remaining attached below the beak to the upper part of the axis; beak 2-10 mm. long; fruiting pedicels reflexed, 5-22 mm. long. Seeds sticky, black, obovoid, 4-8 mm. long, 2 (rarely 1) per locule.

Viscainoa is a genus containing a single species, with two varieties. It is found mainly on the peninsula and Gulf islands of Baja California, but also on Cedros Island, the Sonoran islands of San Esteban and Tiburón, and on the Sonoran mainland near Guaymas at Bahía San Carlos and Miramar.

Viscainoa is morphologically similar, and probably closely related, to *Morkillia* Rose & Painter (*Chitonia* Ses. & Moc. ex DC.), a genus known from Tamaulipas, Hidalgo, Puebla, and Oaxaca on the mainland of Mexico. Katherine Brandegee, in fact, stated (1888, p. 230) that, "Its true place is certainly in *Zygophyllaceae* between *Guaiacum* and *Chitonia*.

and probably a slight modification of the generic character will admit it into the latter genus."

Viscainoa geniculata (Kell.) Greene, Pittonia 1:163. 1888

Staphylea geniculata Kell. Proc. Calif. Acad. 2:22. 1863.

Chitonia simplicifolia Wats. in Orcutt, West. Amer. Sci. 2:58. 1886. *nom. nud.*

KEY TO THE VARIETIES

Leaves simple, usually entire .... 1a. *V. geniculata* var. *geniculata.*
Leaves odd-pinnate; leaflets 3-5, entire .... 1b. *V. geniculata* var. *pinnata.*

1a. V. geniculata var. geniculata

Stipules tomentose, 2-10 mm. long; leaves petiolate or subsessile, simple (occasionally deeply lobed to pinnate with 2-3 leaflets), usually entire, coriaceous, tomentose to lanate, green to yellow-green, ovate or obovate to elliptic, occasionally inequilateral, 5-55 mm. wide, 1-8.5 cm. long, base cuneate, apex obtuse to mucronate or retuse (rarely obcordate); petiole short, to 6 (rarely to 10) mm. long; flowers to 3 cm. in diameter; sepals 4-5, 2-5 mm. wide, 6-10 mm. long; petals 4-6, to 11 mm. wide and 15 mm. long; stamens 4-6 mm. long; capsule to 2 cm. wide and 3.5 cm. long, beak 2-8 mm. long; fruiting pedicel 10-22 mm. long.

Flowering from October to May and fruiting from December to June.

TYPE LOCALITY: Isla Cedros. "It was found growing in sandy ravines, near the sea-shore, on the east side of the Bay of San Sebastian Biscayno [Bahía Vizcaíno], nearly opposite the guano island of Elide" (Kellogg, 1863, p. 22). This collection was made by J. A. Veatch in 1859. The holotype was deposited in the Herbarium of the California Academy of Sciences and presumably was destroyed during the earthquake and fire of 1906. It seems desirable, therefore, to designate an isotype in the Gray Herbarium of Harvard University as lectotype.

REPRESENTATIVE SPECIMENS: 24 mi. S. San Felipe, *Wiggins 15841* (CAS, DS); 1.5 mi. N Puertecitos, *Porter 613* (CAS, DS); 34.5 mi. N Molino de Lacy, *Porter 605* (CAS, DS); Bahía de San Luis Gonzaga, *Johnston 3338* (CAS); Calamajué, *Porter 594* (CAS, DS); upper Arroyo de Calamajué, *Wiggins 16029* (CAS, DS); 29 mi. N Punta Prieta toward Calamajué, *Porter 587* (CAS, DS); 8 mi. E El Rosario, *Wiggins 4332* (DS, GH, UC); near San Fernando, *Orcutt 1344* (GH, UC); 6 mi. E Puerto de Santa Catarina, *Dressler 611* (GH); 4 mi. E El Mármol, *Wiggins 7580* (AAH, DS, UC); between San Agustín & Cataviñá, *Wiggins 5320* (CAS, DS, GH, UC); Cataviñá, *Wiggins 4413* (CAS, DS, GH, UC); 24 mi. SE Laguna Seca Chapala, *Ferris 9021* (DS); 14 mi. NE Punta Prieta toward Desengaño, *Wiggins 7642* (DS, GH, UC); Agua Amarga, *Wiggins 14821* (CAS, DS); 6.5 mi. NW Bahía de los Angeles, *Porter 578* (CAS, DS); Bahía de los Angeles, *Wiggins 7695* (AAH, DS, UC); 12.5 mi. N San Borja, *Porter 562* (CAS, DS); San Borja, *Moran 1988* (DS, UC); 2.5 mi. S Punta Prieta, *Wiggins 15082* (CAS, DS); 15 mi. SW Punta

Prieta, *Epling & Robinson,* 10 Feb. 1935 (DS); 1 mi. from beach 35 mi. S Punta Prieta, *Wiggins 11309* (CAS, DS, GH, UC); 4.5 mi. SE Rosarito, *Porter 554* (CAS, DS); 8 mi. S Rosarito toward Miller's Landing, *Thomas 7980* (DS); Miller's Landing, *Porter 551* (CAS, DS); 15 mi. W Mezquital, *Gentry 7893* (DS, UC); 2 mi. S. Calmallí, *Epling & Robinson,* 6 Feb. 1935 (AAH, DS, UC); 10.2 mi. NW El Arco, *Porter 208* (CAS, DS); Bahía de San Francisquito, *Johnston 3582* (CAS); 17 mi. NW San Ignacio, *Reed 6262* (DS); 8 mi. S El Alamo, *Wiggins & Ernst 604, 605* (CAS, DS); 35.5 mi. S San Ignacio toward La Purísima, *Porter 525* (CAS, DS); 5 mi. N Santa Rosalía, *Gentry 3683* (AAH, UC); coast SE Santa Rosalía, *Moran 7478* (DS, GH); Mulegé, *Palmer 27* (DS, GH, UC); 49.6 km. SE Mulegé, *Carter & Kellogg 2945* (DS, GH); 50.5 km. S El Médano, *Carter, Alexander, & Kellogg 2465* (DS); 19 mi. W Km. 38.5 on new highway W La Paz, *Porter 434* (CAS, DS); La Paz, *Johnston 3052* (CAS, GH), *Jones 24074* (AAH, UC); Bahía Pichilingue, *Porter 390* (CAS, DS); 2 mi. N Bahía Pichilingue, *Porter 419* (CAS, DS); San Pedro, *Moran 7007* (DS); 15.5 mi. S Todos Santos, *Porter 366, 368* (CAS, DS); Isla Ventana, Bahía de los Angeles, *Wiggins 14872* (CAS, DS); Isla Angel de la Guarda, *Moran 8640* (GH); Isla San Lorenzo Norte, *Johnston 4194* (CAS); Isla Tortuga, *Lindsay,* 12 April 1947 (DS); Isla Ildefonso, *Moran 9063* (GH); Isla San José, *Moran 3756* (DS, UC); Isla Partida, *Johnston 3230* (AAH, CAS, GH, UC); Isla Espíritu Santo, *Moran 3684* (DS, UC); Isla Pichilingue, *Jones 27454* (AAH, DS, UC); Isla Cedros, *Veatch,* 1859 (isotype GH); Isla Margarita, *Rose 16303* (GH).

Viscainoa geniculata var. *geniculata* is found on the sandy, usually granitic, soils of arroyo banks, outwash plains, and rocky hillsides from San Matías Pass in the northeast (Goldman, 1916) and near El Rosario in the northwest, throughout Baja California and the islands in the Gulf of California, to 15.5 miles south of Todos Santos in the Cape Region. This variety also occurs on the Sonoran islands of Tiburón, San Esteban, and San Pedro Mártir and on the Sonoran mainland near Guaymas. T. S. Brandegee (1891) reports *Viscainoa geniculata* from San José del Cabo, but herbarium specimens are unknown from this far south.

This evergreen shrub is found throughout the area indicated above, with the exception of the Magdalena Plain, the Central Gulf Coast between Isla Ildefonso and Isla San José, and the Sierra Giganta. It is undoubtedly present in the latter two areas, but has not as yet been collected in these botanically little-known sections of Baja California. It is most common in the northern two-thirds of the Vizcaíno Region between San Ignacio and El Mármol and in the southern part of the lower Colorado Valley between Bahía de los Angeles and San Felipe. It is in this latter area, on the broad, sandy outwash plains between the Arroyo de Calamajué and the Arroyo Miramar, where *Viscainoa*, together with *Larrea tridentata* (Ses. & Moc. ex DC.) Cov. and *Fouquieria splendens* Engelm. become dominant members of the vegetation. It becomes a dominant nowhere else in Baja California, with the exception of a few small islands in the Gulf of California on which it may be the only shrub.

Viscainoa geniculata var. *geniculata* is heavily browsed by cattle (and probably also by goats) when found near inhabited areas, as is the pinnate variety. Michael E. Soulé, a graduate student in herpetology at Stanford University, has observed the chuckwalla *Sauromalus hispidus* climbing up into the shrubs and eating the leaves on several of the small islands near Bahía de los Angeles.

1b. **V. geniculata** var. **pinnata** Johnst., Univ. Calif. Publ. Bot. 7:439. 1922

Viscainoa pinnata Gentry, Madroño 5:161. 1940.

Stipules tomentose to almost glabrate, 2-13 mm. long; leaves petiolate, odd-pinnate; petioles tomentose to glabrate, 2-17 mm. long; leaflets 3-5 (laterals rarely aborting to give 2 or 1), petiolulate (laterals occasionally sessile on the rachis), entire, coriaceous, tomentose to glabrate, green to yellow-green, elliptic to ovate or obovate (occasionally inequilateral), apical leaflet the largest, 5-35 mm. wide, 15-65 mm. long, laterals 5-25 mm. wide, 1-5 cm. long, base cuneate (rarely oblique), apex mucronate to obtuse or retuse (rarely obcordate); flowers ca. 2 cm. in diameter; sepals 5-6, 3-5 mm. wide, 5-8 mm. long; petals 4-5, to 8 mm. wide and 11 mm. long; stamens 7-8 mm. long; capsule to 1.5 cm. wide and 3.5 cm. long, beak 5-10 mm. long; fruiting pedicel 5-12 mm. long.

Variety *pinnata* has a gametic chromosome number of $n = 13$ (*Porter 508*).

Flowering and fruiting following the winter rains.

TYPE LOCALITY: "San Raimonda Creek [Arroyo de San Raymundo], Baja California, April, 1889, *Brandegee*. Sheet No. 109442 in Herb. Univ. Calif." (Johnston, 1922, p. 439).

SPECIMENS EXAMINED: El Carrizal, *Porter 505, 508, 509* (CAS, DS); 8 mi. N San Juanico, *Gentry 4311* (DS, GH, UC); Cadajé, *Porter 510* (CAS, DS); Arroyo de San Raymundo, *Brandegee*, April, 1889 (UC!), *Constance 3140* (UC), *Porter 511* (CAS, DS), *Thomas 8366* (DS, GH); Arroyo de San Juan, *Porter 513* (CAS, DS); 4.5 mi. NW Arroyo de San Juan, *Porter 517* (CAS, DS).

This pinnate variety of *Viscainoa geniculata* is common in and along a series of sandy arroyos on the west coast of Baja California, near Lat. 26° 10′ N, Long. 112° 30′ W., between El Carrizal on the south and 4.5 miles northwest of

Arroyo de San Juan on the north, a distance along the road of about 24 miles. All of these arroyos appear to arise at a common point to the east in the Sierra de las Palmas.

Pinnate leaves are found occasionally on *Viscainoa geniculata* var. *geniculata, e. g.: Moran 3756; Orcutt 1344; Porter 419, 434, 578,* and *587;* and *Wiggins 15082.* Leafy branches of the typical variety are also commonly found that have several leaves arising from the same axis on a stem; and *V. geniculata* var. *pinnata* will have an occasional entire leaf, *e. g.: Constance 3140; Gentry 4311;* and *Porter 508, 513,* and *517.* However, none of these collections is an example of the presence of one variety within the distributional area of the other; the nearest *V. geniculata* var. *geniculata* known to the territory of *V. geniculata* var. *pinnata* is 35.5 miles south of San Ignacio, still 35.5 miles north of the nearest collection of the pinnate variety.

Further field work is needed to determine the nature and extent of the geographic and reproductive isolation of these two taxa.

2. **Guaiacum** L., Sp. Pl. **1**:381. 1753

Trees or shrubs 1-10 m. high with hard resinous wood and stout branches with swollen nodes. Stipules minute, usually caducous. Leaves opposite, petiolate, even-pinnate, to 10 cm. long. Leaflets 1-6 pairs, subsessile on the rachis, coriaceous, glabrous to pubescent, linear to broadly obovate, apex rounded to mucronate, to 16 cm. long. Flowers 1-many, pedunculate from the axils of minute deciduous bracts, to ca. 3 cm. in diameter. Sepals 4-5, unequal, free to somewhat united at the base, oblong to orbicular, deciduous. Petals 4-5, blue or purple (rarely white), obovate, apex rounded to mucronate. Stamens 8-10; filaments subulate or the lower half slightly winged; anthers oblong, cordate, or sagittate. Ovary 2-5-lobed, 2-5-loculed, obovate or clavate, glabrous to tomentose, on a short gynophore 1-3 mm. long; ovules 8-10 per locule, pendulous; style forming a slender subulate beak ca. 5 mm. long on the young fruit; stigma entire or with as many lobes as locules in the ovary. Fruit a smooth, coriaceous, green to orange or reddish, ellipsoid to obovoid, septicidal capsule 1-2 cm. broad, 1-2 cm. long, angles winged. Seeds 1 per locule.

TYPE SPECIES: *Guaiacum officinale* L.

A New World genus consisting of some six species found from Sonora, Mexico, to the Guianas and throughout the West Indies to southern Florida. A single endemic species is known from Baja California.

1. **Guaiacum unijugum** T. S. Brandg., Univ. Calif. Publ. Bot. 6:183. 1915

A divaricate woody shrub growing to ca. 2 m. high; bark brownish-gray; youngest branches pubescent, older glabrate; stipules caducous; leaves yellow-green, crowded on short lateral branchlets 3-5 mm. long; leaflets 1 (rarely 2) pair, tomentose to almost glabrate, ovoid, mucronate, base oblique, 3-10 mm. wide, 6-13 mm. long; rachis 1-8 mm. long, tipped by a small caducous tomentose spine ca. 1 mm. long; petioles and rachises densely pubescent; flowers pedunculate from the axils of minute bracts on the lateral branchlets, 1-4 per branchlet, to 1.5 cm. in diameter; pedicels 6-13 mm. long, pubescent; sepals 5, green, free, puberulent, oblong to obovate, rounded at the apex, 2-4 mm. wide, 3-6 mm. long; petals 5, clear blue drying to yellow, to 6 mm. wide and 12 mm. long; stamens 10, 7-8 mm. long; filaments subulate; anthers subbasifixed, curved, sagittate, ca. 2 mm. long; ovary obovate, 5-lobed, 5-loculed, tomentose, on a short gynophore ca. 1 mm. long; ovules ca. 8 per locule, in 2 rows on the placenta, placentation axile; style slender, subulate, less than 1 mm. long; stigma entire; fruit a yellow-brown mucronate tomentose capsule, to ca. 2 cm. long; fruiting pedicels 7-16 mm. long; rarely more than 1 seed maturing per fruit.

Flowering in August and fruiting in August and September.

TYPE LOCALITY: "Collected by T. S. Brandegee near San José del Cabo, Baja California. Type, Herb. Univ. Calif. No. 109558" (T. S. Brandegee, (1915, p. 183).

SPECIMENS EXAMINED: Bahía de los Frailes, *Chambers 865* (DS, UC); San José del Cabo, *Brandegee*, 5 Sept. 1890 (UC!), *Grabendorfer*, 1899 (UC).

This rare and little-known endemic from the southeastern Cape Region differs from *Guaiacum coulteri* Gray var. *coulteri*, found from Sonora to Oaxaca, and from *G. coulteri* var. *palmeri* (Vail) Johnst., known from the vicinity of Carbó, Sonora, to San Blas in northwestern Sinaloa, in its smaller flowers and single pair of ovoid tomentose leaflets. The flowers of *G. coulteri* are up to twice the size of those of *G. unijugum*, and its leaves are 2-6 cm. long with 6-10 linear-oblong to elliptic-oblong glabrous leaflets that are 3-10 mm. wide and 10-25 mm. long. *G. unijugum* is probably closely related to *G. coulteri*, and further collections and morphological and cytological investigation may prove it to be a subspecies or variety of the latter. On the basis of present information, however, it is best to retain Brandegee's name, rather than to make a new combination.

Chambers collected *Guaiacum unijugum* on "Sand dunes, Los Frailes Bay," and it is probably restricted to the coastal sand dunes and sandy washes in this area and to those near

San José del Cabo, about 30 miles to the south. This distribution falls into an arid and botanically little-known southern extension of the Central Gulf Coast subdivision of the Sonoran Desert, which extends from the vicinity of Punta Arena del Sur to San José del Cabo, a distance of roughly 40 miles. *G. unijugum* is thus separated from the Mexican mainland and its nearest congeners by the mouth of the Gulf of California, a distance of about 200 kilometers.

3. **Larrea** Cav., An. Hist. Nat. Madrid 2:119. 1800

Strong-scented, divaricately-branched, resinous shrubs to 4 (rarely to 7) m. high; younger branches quadrangular in cross-section and pubescent, older cylindrical and glabrate; nodes swollen, internodes short, 1-2 cm. long. Stipules fleshy, reddish, triangular, pubescent, obtuse to short-acuminate, 1-4 mm. long, persistent; glands on the inner surface secreting a resin making the plants highly glutinous at times. Leaves opposite, sessile to short-petiolate, pinnately lobed or with 2 more or less connate leaflets. Leaflets coriaceous, green to olive-brown, pubescent to glabrate. Flowers solitary, to ca. 2.5 cm. in diameter; pedicels pubescent, 3-15 mm. long. Sepals 5, free, unequal, ovoid, acute to obtuse, pubescent, persistent to deciduous. Petals 5, bright yellow, ovoid, acute or rounded to variously incised at the apex. Stamens 10, 5-10 mm. long, inserted on the small 10-lobed disc; filaments filiform to subulate, adnate at the inner base to a 2-lobed or irregularly laciniate membranaceous scale nearly as long as the filament; anthers oblong, sub-basifixed, sagittate, 1-3 mm. long. Ovary deeply 5-lobed, 5-loculed, globose, on a short gynophore ca. 1 mm. long densely pubescent, 2-5 mm. long; style subulate to cylindric, 2-6 mm. long; stigma simple to slightly 5-lobed. Fruit a 5-lobed, 5-loculed, densely pubescent, globose, septicidal capsule, ca. 7 mm. long. Carpels 1-seeded, dehiscent or indehiscent at maturity.

TYPE SPECIES: *Larrea nitida* Cav.

A New World genus of five species, four in the arid regions of Argentina (two of these also ranging into Peru, Bolivia, or Chile), and one in the warm deserts of North America.

1. **Larrea tridentata** (Ses. & Moc. ex DC.) Cov., Contr. U. S. Nat. Herb. 4:75. 1893

Zygophyllum tridentatum Ses. & Moc. ex DC., Prodr. 1:706. 1824.

Larrea mexicana Moric., Pl. Nouv. Amér. 71. 1839.

Guaiacum mexicanum (Moric.) Baill., Bot. Med. 2:886. 1844.

Zygophyllum californicum Torr. & Frém. in Frém., Second Rep. 257. 1845. *nom. nud.*

Larrea glutinosa Engelm. in Wisliz., Mem. Tour No. Mex. 93. 1848.

Zygophyllum resinosum Berl. in Berl. & Chovel, Diario de Viaje 52. 1850. *nom. nud.*

Covillea divaricata (Cav.) Vail, Bull. Torr. Bot. Club **22**:229. 1895. In part.

Covillea tridentata (Ses. & Moc. ex DC.) Vail, Bull. Torr. Bot. Club **26**:302. 1899.

Covillea glutinosa (Engelm. in Wisliz.) Rydb. in Vail & Rydb., N. Amer. Fl. **25**:108. 1910.

Larrea tridentata var. *glutinosa* Jeps., Manual 604. 1925.

Schroeterella glutinosa (Engelm. in Wisliz.) Briq., Ver. Geobot. Inst. Zürich **3**: 664. 1925.

Schroeterella tridentata (Ses. & Moc. ex DC.) Briq., *loc. cit.*

Neoschroetera glutinosa (Engelm. in Wisliz.) Briq., Candollea **2**:514. 1926.

Neoschroetera tridentata (Ses. & Moc. ex DC.) Briq., *loc. cit.*

Ultimate branchlets appressed-pubescent with short white hairs; young branches with reddish bark, bark gray or blackish on older branches; black-banded and crooked at the nodes, banding caused by the resinous excresence of the persistent stipules; stipules obovoid, acute to short-acuminate, spreading or at least not clasping the stem, 1-4 mm. long; leaves subsessile to short-petiolate, petiole to ca. 2 mm. long; leaflets 2, entire, divaricate, connate to each other and adnate to the rachis for 2-4 mm. at the base, obliquely lanceolate to falcate, inequilateral, mucronate, coriaceous, glutinous, densely appressed-pubescent to glabrate, 1-8.5 mm. wide, 4-18 mm. long; a pubescent, green, deciduous mucro to 2 mm. long on the end of the rachis between the leaflets; flowers to ca. 2.5 cm. in diameter, pedicels 3-12 mm. long; sepals appressed-pubescent, 3-4.5 mm. wide, 5-8 mm. long; petals oblong to oblanceolate, the short claw brownish, 2.5-5.5 mm. wide, 7-11 mm. long, twisted at the claw and appearing propeller-like; stamens 5-9 mm. long; filaments 4-8 mm. long, the scale ½ to as long as the filament, to 3 mm. wide; anthers 2-3 mm. long; hairs on the ovary 2-4 mm. long, carpels attached only on inner angle; ovules ca. 8 per locule, placentation axile; style cylindric, 4-6 mm. long, persisting on the young fruit; stigma minutely and obscurely lobed; fruit pilose-wooly, hairs silvery turning reddish-brown with age; fruiting pedicel 4-13 mm. long; seeds brown, boat-shaped, 4 mm. long.

A somatic chromosome number of $2n = 52$ has been reported for *Larrea tridentata* (Covas, 1949). Numbers have also been reported for the South American members of the genus, with the exception of *L. ameghinoi* Speg.: *L. cuneifolia* Cav., $2n = 52$ (Covas & Schnack, 1946); *L. divaricata* Cav., $2n = 26$ (Covas & Schnack, 1946); and *L. nitida* Cav., $2n = 26$ (Covas, 1949; Rahn, 1960). Somatic numbers of $2n = 52$ for *L. divaricata*, $2n = 52$ for *L. nitida*, and $2n = 104$ for *L. tridentata* listed by Darlington and Wylie (1955) are actually tetraploid counts (Porter, 1961).

In Baja California flowering from September to May and fruiting from September to June.

TYPE LOCALITY: "In regno Mexicano" (DeCandolle, 1824, p. 706). The holotype is presumably in the Herbier DeCandolle, Geneva.

REPRESENTATIVE SPECIMENS: La Rumorosa, *Cota*, March, 1932 (UC); 12 mi. W Mexicali, *Porter 618* (CAS, DS); Seven Wells, *Mearns & Schoenfeldt 2872* (DS); Laguna Gardner, *Mearns & Schoenfeldt 2910* (DS); San Matías Valley, *Robertson 4* (UC); between La Ventana Pass & San Felipe, *Wiggins 13011* (DS, GH); between El Cajon & Algadones, *Wiggins 9844* (DS); 13 mi. S San Felipe, *Porter 616* (CAS, DS); 13.5 mi. N Puertecitos, *Porter 614* (CAS, DS); 15 mi. S Puertecitos, *Porter 611* (CAS, DS); 3 mi. NE Las Arrastras, *Porter 602* (CAS, DS); 1.5 mi. NW Calamajué, *Porter 596* (CAS, DS); 15 mi. NE El Rosario toward El Sauzalito, *Porter 156* (CAS, DS); 32 mi. E El Rosario toward San Agustín, *Ferris 8551* (DS); Missión San Fernando, *Harvey*, 13 April 1954 (UC); El Mármol, *Wiggins 4368* (AAH, DS, GH, UC); Cataviñá, *Wiggins 4412* (AAH, CAS, DS, GH, UC); 15.5 mi. S Rancho Laguna Chapala, *Porter 179* (CAS, DS); Desengaño, *Porter 584* (CAS, DS); 6.5 mi. NW Bahía de los Angeles, *Porter 577* (CAS, DS); Bahía de los Angeles, *Wiggins 7693* (AAH, DS, UC); 12.5 mi. N San Borja, *Porter 561* (CAS, DS); 3.5 mi. W San Ignacito toward Rosarito, *Porter 200* (CAS, DS); 30 mi. N Mezquital, *Hammerly 66* (CAS, DS); 17.6 km. S Mezquital, *Carter & Kellogg 2979* (DS, GH); 5 mi. W Calmallí, *Thomas 7974* (DS, GH); 5 mi. W El Barril, *Wiggins 7832* (AAH, DS, UC); 12 mi. SW El Arco toward La Banderita, *Thomas 8273* (DS); 2.5 mi. NW La Cantina, *Porter 537* (CAS, DS); 5 mi. W Los Mártires, *Porter 530* (CAS, DS); 40 mi. NW San Ignacio toward El Arco, *Porter 209* (CAS, DS); 23.5 mi. S San Ignacio toward Cuarenta, *Porter 527* (CAS, DS); 6 mi. N Cuarenta, *Thomas 8357* (DS, GH); 13.5 mi. NW Arroyo de San Juan, *Porter 519* (CAS, DS); El Carrizal, *Porter 507* (CAS, DS); Arroyo de Mezquital, *Porter 503* (CAS, DS); Río de la Purísima at ford of San Ignacio road, *Porter 496* (CAS, DS); 4.5 mi. NW Santa Rosalía, *Porter 217* (CAS, DS); 35 mi. S Mulegé, *Porter 230* (CAS, DS); Comondú, *Brandegee*, Feb. 1889 (UC); 15.5 mi. SW San José Comondú, *Porter 233* (CAS, DS); Loreto, *Jones 27085* (AAH, DS, UC); 30 mi. NW El Crucero, *Porter 485* (CAS, DS); 29 mi. S El Crucero, *Porter 450* (CAS, DS); 9.5 m. NE Estero Salinas toward Llanos de Hiray, *Porter 468* (CAS, DS); 8.5 mi. NW Santa Rita toward Llanos de Hiray, *Porter 472* (CAS, DS); 81 mi. NW La Paz, *Porter 447* (CAS, DS); 42.5 mi. W La Paz, *Porter 440* (CAS, DS); 19 mi. W Km. 38.5 on main highway W La Paz, *Porter 433* (CAS, DS); 3.5 mi. W Km. 38.5, *Porter 436* (CAS, DS); 11 mi. W main highway toward Arroyo Seco, *Porter 427* (CAS, DS); 15 mi. W La Paz, *Hammerly 201* (CAS, DS, GH); Los Aripes, *Porter 422* (CAS, DS); 10.5 mi. SE La Paz airport toward Todos Santos, *Porter 453* (CAS, DS); Isla San Luis, *Johnston 3323* (CAS, GH); Isla Angel de la Guarda, *Johnston 3403* (CAS); Isla San Marcos, *Ferris 8662* (DS); Isla Carmen, *Rose 16649* (GH); Isla San Francisco, *Moran 3741* (DS, UC).

T. S. Brandegee (1891) reported *Larrea tridentata* from Todos Santos, but herbarium specimens are known from no further south than 10.5 miles southeast of La Paz airport, about 43 miles north of Todos Santos. *L. tridentata* is rare in the region south of La Paz, but it is quite possible that the plant ranges along the arid western coast of the Cape Region nearly to Todos Santos. The plant has also been reported from San Luis Gonzaga Bay, San Francisquito Bay, and Guadalupe Point (Johnston, 1924).

The total distribution of this species is discussed by Shreve (1940), Rzedowski and Medellín Leal (1958), and Garcia, Soto, and Miranda (1960).

There has been much controversy as to whether the North American *Larrea tridentata* is specifically distinct from the South American *L. divaricata* Cav. Vail (1895) was the first to argue that the two are conspecific, but she soon reversed herself (1899) upon examining a larger series of South American collections. Since Vail's paper in 1895, there have been a number of authors arguing for and against the distinctness of *L. tridentata*. Johnston (1924, 1940), Monticelli (1939), Axelrod (1950), and Morello (1958) have considered the two as identical, while Robinson (in Gray, 1897), Garcia, Soto, and Miranda (1960), and Ragonese (1960) have regarded them as distinct.

A careful comparison of North and South American material reveals that the two are readily separable on the basis of leaflet and stipule characteristics, as has been pointed out by Robinson (in Gray, 1897) and Vail (1899).[2] Not only does the herbage of *Larrea divaricata* tend to be more copiously pubescent than that of *L. tridentata*, but the edges and veins of the leaflets of *L. divaricata* are lined with many white hairs 1-2 mm. long that are clearly discernible with the unaided eye. Leaflet veins in *L. tridentata* may at times be conspicuous, but they are usually dark, not lined with hairs. Occasional specimens of *L. tridentata* do, however, have some leaflets with the white-hairy veins and hairiness on the edges of the leaflets characteristic of *L. divaricata*, so this is not as infallible a criterion in separating the two species as are the following. There is a distinct difference between the two in the shape of the leaflets, those of *L. tridentata* being obliquely lanceolate to falcate, while those of *L. divaricata* are obovate to ellipsoid, the tips rarely curving toward one another. The stipules of *L. tridentata* are obovoid, acute to short-acuminate at the apex, 1-4 mm. long, and dis-

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[2] Differences in the internal petiolar and foliar anatomy are discussed by Ragonese (1960).

tinctly free to spreading from the stem or petioles (as they are also in the South American *L. cuneifolia* and *L. nitida*). The stipules of *L. divaricata,* on the other hand, are broadly ovate, obtuse or rounded at the apex, 1-2 mm. long, and distinctly clasping the stem.

The two taxa overlap in many of their morphological variations. The differences discussed above, the geographic distributions of the taxa, and the differences in chromosome number, however, provide sufficient evidence for considering them to be separate species.

Larrea tridentata is found throughout the desert regions of Baja California, with the exception of the southeastern tip of the Cape Region. The species occurs on alluvial and volcanic soils, sandy plains, and the edges of alkali flats, being rarely found on granitic soils. It is found as a dominant and in many associations throughout arid Baja California wherever edaphic factors and the lack of competition are favorable. *L. tridentata* never occurs, however, in such extensive stands as those in the Lower Colorado Valley. A possible exception is that in the valley surrounding Laguna Seca Chapala.

4. **Fagonia** L., Sp. Pl. **1**:386. 1753

Prostrate-spreading to upright diffusely branched suffrutescent annual or perennial herbs or subshrubs, to 8 dm. high and 1.5 m. in diameter; branches angled at the occasionally minutely spinulose nodes, striate, green, yellowing with age; bark on oldest branches gray; herbage glandular, pubescent, or glabrous, occasionally tinged with purple. Stipules subulate to acerose, reflexed to spreading or ascending, spinescent with a white tip, to 2 cm. long; occasionally making the plant quite prickly to the touch. Leaves opposite, compound, digitately 3-7-foliolate; leaflets entire, coriaceous, petiolulate, linear to broadly ovate, spinescent with a white tip; apical leaflet the largest, to 2 cm. wide and 3 cm. long; lateral leaflets usually inequilateral, often caducous. Flowers solitary, axillary, few to many, 1-1.5 cm. in diameter; pedicels thin, to 1.5 cm. long. Sepals 5, free, lanceolate to oblong, green to purple, spinescent with a white tip, deciduous. Petals 5, pink to dark red-purple (rarely white), spatulate, mucronate. Stamens 10; filaments filiform; anthers sub-basifixed, sagittate, 0.5-1 mm. long. Ovary 5-lobed, 5-loculed, ovoid or obovoid, stipitate glandular and pubescent to pubescent or glabrous, sessile or essentially so, 1-2 mm. in diameter; ovules 2 per locule, placentation basal; style subulate, to 4 mm. long, persisting to form a beak on the fruit; stigma minutely and obscurely lobed. Fruit a moderately inflated, deeply 5-lobed, 5-loculed, obovoid, loculicidal capsule, glandular and pubescent to pubescent or glabrous, coriaceous, reticulate, to 7 mm. wide and 5 mm. high, green, yellowing with age; beak thickened at the base, commonly twisted clockwise, to 4.5 mm. long; fruiting pedicel abruptly reflexed; carpels separating at the inner angle, but remaining attached below the beak to the upper part of the axis, dehiscing ventrally, the shiny glutinous endocarp separating from the coriaceous exocarp. Seeds 1 or 2 per locule, dark, flattened, ovate, shiny, minutely reticulate, to 2.5 mm. wide and 4 mm. long.

TYPE SPECIES: *Fagonia cretica* L.

Fagonia is a genus known from the warm arid regions of all continents except Australia.

There has been some controversy concerning the status of *Fagonia* in North America. Bentham (1844), Standley (1911), and Johnston (1924, 1924a) have shown that the *Fagonia* of the New World are separable from the Old World members of the genus, but Johnston, differing from Bentham and Standley, assigned both the North and South American taxa (with the exception of *F. densa*) to the South American *Fagonia chilensis* H. & A. An examination of the available South American material, however, shows the North American taxa to be specifically distinct from the South American species of the genus.

Standley (1911) emphasized glandularity and pubescence in his treatment of the genus, while Johnston (1924) emphasized stipular development. A combination of these characters is used in the following treatment. Absolute sizes, however, are not reliable, as there is quite a difference in vegetative growth from year to year, depending upon precipitation; those plants growing with little water apparently also tend to be less open and more bushy in habit. Amount of pubescence or glandularity probably is dependent partially upon precipitation, but the type of pubescence and stipule type are constant. The difference in leaflet size on the same plant is also striking. The young leaflets near the ends of the branches may be linear and scarcely 2 or 3 millimeters long, while the older basal leaflets may be 2 centimeters long and a centimeter wide, or larger.

The flowering and fruiting dates given below have been compiled from herbarium collections. There is a good possibility, however, that *Fagonia* produces flowers whenever there has been sufficient rain.

KEY TO THE SPECIES

Leaflets 5-7-foliolate .... 1. *F. palmeri.*

Leaflets 3-foliolate

Stipules acerose, ascending, as long as or longer than the petioles .... 2. *F. densa.*

Stipules subulate to linear-subulate, reflexed to spreading, not as long as the petioles

Stipules subulate, rarely spreading, usually 1-3 (never over 6) mm. long; plants upright to prostrate; flowers to ca. 1 cm. in diameter

Branches with small stipitate glands to glabrous

Leaflets glandular; branches rarely scabrous; fruits and ovaries puberulent and glandular .... 3. *F. californica.*

Leaflets glabrous; branches soon scabrous; fruits and ovaries puberulent, but never glandular .... 4. *F. laevis.*

Branches villous, never glandular .... 5. *F. villosa.*

Stipules linear-subulate, rarely reflexed, to 8 mm. long or longer; plants prostrate-spreading; flowers to ca. 1.5 cm. in diameter

Branches with large (1 mm. in diameter) short-stipitate to subsessile glands, glabrous toward the base .... 6. *F. pachyacantha.*

Branches with small (½ mm. in diameter and less) stipitate glands and many straight glandless hairs, more glands toward apices, more hairs toward bases .... 7. *F. barclayana.*

1. **Fagonia palmeri** Vasey & Rose, Contr. U. S. Nat. Herb. 1:82. 1890

Fagonia chilensis var. *palmeri* (Vasey & Rose) Johnst., Proc. Calif. Acad., ser. 4, **12**:1052. 1924.

Flat-topped to rounded, prostrate to upright, to 0.5 m. high and 1 m. in diameter; herbage densely covered with small stipitate glands, older branches becoming glabrate; stipules acerose, ascending, 2-9 mm. long; leaflets 5-7 (occasionally 1 or more aborting), subfleshy, flattened, linear to linear-lanceolate, to 1 mm. wide, 2-14 mm. long; petioles 4-12 mm. long; flowers to ca. 1.5 cm. in diameter; pedicels 2-7 mm. long, glandular-stipitate; sepals oblong-lanceolate, glandular-stipitate, 1.5-2.5 mm. wide, 4-5 mm. long; petals rose, 2-4 mm. wide, 5-8 mm. long; filaments 4 mm. long; ovary pubescent, style 2-3.5 mm. long; fruiting pedicels 3-8 mm. long; fruit puberulent and glandular, 4-6 mm. in diameter, 4-5 mm. high; beak 3-4 mm. long; seeds 1 per locule.

This species has a gametic chromosome number of $n = 10$ *(Moran 8795).*

Known to flower and fruit from March to May.

TYPE LOCALITY: "Santa Rosalia. Lower California." McVaugh (1956, p. 314) states that, "According to Palmer's field notes, Nos. 197-210, inclusive, were collected in a range of mountains ('contiguous to Santa Rosalía') made up entirely of pure gypsum."

SPECIMENS EXAMINED: Santa Rosalía, *Ferris 8703* (DS, NY), *Palmer 209* (US!; isotypes CAS, GH, NY, UC);Isla San Marcos. *Ferris 8639* (DS, NY), *Johnston 3612* (CAS, DS, GH, NY, UC), *Moran 3964* (DS, UC)

This species is locally abundant in washes and on gypsum hills and cliffs on Isla San Marcos and on the peninsula near Santa Rosalía. It has also been collected on Isla Tiburón, Sonora [*Moran 8795* (GH)].

2. **Fagonia densa** Johnst., Proc. Calif. Acad., ser. 4, 12:1052. 1924

Dense, compact, upright, globose subshrub, to 80 cm. high and 1 m. in diameter; herbage densely covered with small short-stipitate and subsessile glands, becoming glabrate with age; younger herbage highly glutinous; stipules acerose to linear-lanceolate, ascending, 3-21 mm. long; the numerous crowded leaves and stipules appearing together as whorled acerose leaves; leaflets 3 (rarely 4) acerose to linear-lanceolate, to 1 mm. wide, 1-11 mm. long, deciduous; petioles 3-18 mm. long; flowers to ca. 1.5 mm. in diameter; pedicels 2-3 mm. long; sepals oblong-lanceolate to oblong, green to yellow, 1.5 mm. wide, 4-5 mm. long; petals pink to purple, 2-4 mm. wide, 6-9 mm. long; filaments 4-5 mm. long; ovary pubescent and with small subsessile glands, style 3-4 mm. long; fruiting pedicels 2-7 mm. long; fruit puberulent and glandular, ca. 6 mm. in diameter, 4-5 mm. high; beak 3-4.5 mm. long; seeds 2 per locule.

This species has a gametic chromosome number of $n = 10$ (*Moran 8590, 8904,* and *10368*).

Known to flower and fruit from March to June.

TYPE: "No. 1285, Herb. Calif. Acad. Sci., collected May 9, 1921, by I. M. Johnston (no. 3532) from gypsum soil in a cañon on *South San Lorenzo Island, Gulf of California*" (Johnston, 1924, p. 1052).

SPECIMENS EXAMINED: San Francisquito, *Brandegee*, 13 May 1889 (UC); Bahía de los Angeles, *Moran 10368* (GH), *Porter 572* (CAS, DS), *Wiggins 14888* (CAS, DS); Isla Angel de la Guarda, *Moran 7234, 8184* (DS), *8590* (GH); Isla San Lorenzo Sur, *Johnston 3532* (CAS!, isotypes GH, NY, UC), *Moran 8904* (GH).

Fagonia densa is found in the southern part of the Lower Colorado Valley and on several islands in the Gulf of California opposite this botanically poorly known area. Recent botanical exploration has revealed it to be much more common than previous records indicated.

3. **Fagonia californica** Benth., Bot. Sulph. 10. 1844

Fagonia californica var. *hindsiana* Benth., *loc. cit.*

Fagonia rosei Standl., Proc. Biol. Soc. Wash. 24:247. 1911.

Fagonia cretica var. *californica* (Benth.) Engl. in Engl. & Drude, Veg. der Erde 9(3):731. 1915.

Fagonia chilensis var. *rosei* (Standl.) Johnst., Proc. Calif. Acad., ser. 4, 12:1051. 1924.

Fagonia californica ssp. *rosei* (Standl.) Wiggins, Contr. Dudley Herb. 4:19. 1950.

Prostrate-spreading; herbage densely covered with small stipitate glands and occasional glandless hairs, becoming glabrate and older branches becoming scabrous; stipules subulate, reflexed to spreading, 1-5 mm. long; leaflets 3, elliptic to oblong-lanceolate or oblong, glandular, soon becoming glabrate, apical leaflet to 12 mm. wide and 18 mm. long, lateral leaflets to 9 mm. wide and 15mm. long, laterals commonly caducous; petioles 1-17 mm. long; flowers to ca. 1 cm. in diameter; pedicels 1-6 mm. long; sepals oblong-lanceolate, glandular, becoming glabrate, green to purple, 1-1.5 mm. wide, 2-3.5 mm. long; petals pink to dark red-purple, 2-4 mm. wide, 5-7 mm. long; filaments ca. 4 mm. long; ovary pubescent and glandular, style 2 mm. long; fruiting pedicels 2-10 mm. long; fruit puberulent and glandular, 3-7 mm. wide, 3-5 mm. high, beak 1.5-2.5 mm. long; seeds 1 per locule.

Flowering from September to April and fruiting from November to April.

TYPE LOCALITY: "Bay of Magdalena, Lower California" (Bentham, 1844, p. 10).

SPECIMENS EXAMINED: Arroyo de San Juan, *Porter 514* (DS); La Purísima, *Wiggins 15010A* (DS); Bahía Magdalena, *Brandegee s. n.* (DS), *Hinds, 1841* (K!); Isla Magdalena, *Brandegee*, 12 Jan. 1889 (GH, UC), *Lung 24* (UC), *Orcutt 7* (GH, NY); Isla Margarita, *Johansen 611* (CAS, DS); 1.5 mi. SE Santa Rita, *Porter 480* (CAS, DS); 92 mi. NW La Paz, *Porter 479* (CAS, DS); 89 mi. NW La Paz, *Porter 448* (CAS, DS); 76.5 mi. NW La Paz, *Porter 444* (CAS, DS).

Fagonia californica occurs in sandy and rocky soils from Arroyo de San Juan south across the Magdalena Plain to its southern boundary. Standley (1911), in his monograph of *Fagonia* in North and South America, considered typical *Fagonia californica* to extend from southern Baja California to southwestern Utah. An examination of a few of the specimens cited therein as *F. californica* (*Abrams 3500; Hall 2794; Jones*, 19 April 1906; *Jones 3641;* and *Palmer 818*) shows them to be Standley's own *Fagonia laevis*. Standley considered *F. laevis* to be completely glabrous, and *F. californica* to have small stipitate glands. However, a thorough study of North American *Fagonia* shows that the former varies from glabrous to slightly glandular, with small stipitate glands usually on pedicels and sepals, occasionally on stipules and petioles, and rarely on the ultimate branches. The branches soon become scabrous, and the fruits are never glandular. *F. californica*, on the other hand, is densely glandular and has small stipitate glands on the fruits; occasionally the entire plant is covered with glands.

Specimens of *F. rosei* from Isla Tiburón, Sonora, (*Johnston 3528* (CAS, GH) and *Rose 16779A* (US!)) are small-leaved, scabrous examples of *F. californica*. This is the only place outside of Baja California that *F. californica* is known to occur.

4. **Fagonia laevis** Standl., Proc. Biol. Soc. Wash. 24:249. 1911

Fagonia chilensis var. *aspera* (Gay) Johnst., Proc. Calif. Acad., ser. 4, 12:1051. 1924. In part.

Fagonia chilensis var. *laevis* (Standl.) Johnst., *loc. cit.*

Fagonia californica ssp. *laevis* (Standl.) Wiggins, Contr. Dudley Herb. 4:19. 1950.

Upright to spreading, to 2 ft. high and 3 ft. in diameter; essentially glabrous, but pedicels and sepals and occasionally stipules and petioles and rarely ultimate branches with small stipitate glands, some specimens entirely glabrous; older branches scabrous (younger parts occasionally scabrous as well); older branches becoming stoloniferous, bearing many erect smaller branches; stipules subulate, reflexed to spreading, 1-6 mm. long; leaflets 3, linear-elliptic, apical leaflet to 5 mm. wide and 18 mm. long, lateral leaflets to 3 mm. wide and 15 mm. long, one or both laterals commonly caducous; petioles 2-15 mm. long; flowers to ca. 1 cm. in diameter; pedicels 1.5-11 mm. long; sepals elliptic to lanceolate, green to purple, ca. 1 mm. wide, 2-3 mm. long; petals pink to dark red-purple, 1.5-3 mm. wide, 4-7 mm. long; filaments 3-4.5 mm. long; ovary glabrous to pubescent, style 1-2 mm. long; fruiting pedicels glabrous to glandular, 1.5-11 mm. long; fruit glabrous to puberulent, 3-6 mm. wide, 4-5 mm. high; beak 1.5-2 mm. long; seeds 1 per locule.

Flowering and fruiting from October to July.

TYPE LOCALITY: "Type in the U. S. National Herbarium, No. 855, 582, collected near Yuma, Arizona, April 25, 1906, by Marcus E. Jones" (Standley, 1911, p. 249).

REPRESENTATIVE SPECIMENS: Arroyo La Agua Amarga, *Wiggins 9928* (DS); 35 mi. S Puertecitos, *Porter 606A* (CAS, DS); Bahía San Luis Gonzaga, *Johnston 3346* (CAS); 2 mi. N Las Arrastras, *Wiggins 15929* (CAS, DS); 8 mi. SE El Rosario, *Wiggins 5255* (CAS, DS, GH, NY, UC); San Fernando, *Cronemiller 3065* (DS); Arroyo de Cataviñacito, *Porter 169, 176* (CAS, DS); 34 mi. N Laguna Chapala toward San Felipe, *Wiggins & Ernst 678* (CAS, DS); 6 mi. S Laguna Chapala, *Wiggins 15054* (CAS, DS); 29 mi. N Punta Prieta, *Wiggins 15059* (CAS, DS); 19.5 mi. N Punta Prieta, *Porter 585* (CAS, DS); 8 mi. SE Desengaño, *Porter 580* (CAS, DS); 9 mi. NW Bahía de los Angeles, *Porter 579* (CAS, DS); Bahía de los Angeles, *Palmer 546* (NY); 6.5 mi. N San Borja, *Porter 560* (CAS, DS); 12 mi. NE Rosarito toward San Borja, *Porter 557* (CAS, DS); main road 4.7 mi. E Miller's Landing, *Porter 552* (CAS, DS); 5 mi. N Mezquital Grande, *Haines & Stewart*, 9 Feb. 1935 (DS, GH, NY, UC); 2 mi. E Mezquital, *Shreve 6960* (GH); 30 mi. inland from Lagoon Head, *Palmer 818* (CAS, GH, UC); Calmallí, *Epling & Robinson*, 5 Feb. 1935 (DS, NY, UC); 4 km. NW El Arco, *Carter, Alexander, & Kellogg 1916* (DS, UC); Santa Gertrudis, *Purpus 112* (DS); 4-5.5 mi. SW El Arco toward La Banderita, *Thomas 8289* (DS); 5.5 mi. S El

Arco, *Wiggins & Ernst 643* (CAS, DS); 15 mi. S El Arco, *Wiggins 11348* (DS, GH, UC); Bahía San Bartolomé, *Rose 16235* (NY): Las Tinajas, *Gentry 7612* (DS, UC); 1.5 mi. SW Los Mártires, *Thomas 8319* (DS); 17.5 mi. S San Ignacio, *Porter 528* (CAS, DS); 47.5 mi. S San Ignacio, *Porter 522* (CAS, DS); 59 mi. S San Ignacio, *Porter 520* (CAS, DS); Arroyo de San Juan, *Porter 515* (CAS, DS); 3 mi. SW Río de la Purísima toward road to Comondú, *Porter 500* (CAS, DS); 2 mi. E San Ignacio, *Porter 212* (CAS, DS); 13.5 mi. NW Santa Rosalía, *Porter 213* (CAS, DS); 4.5 mi. NW Santa Rosalía, *Porter 216* (CAS, DS); Santa Rosalía, *Palmer 196* (GH); 4.8 mi. W Santa Rosalía toward Santa Agueda, *Wiggins 7946* (DS); 7 mi. S Santa Rosalía, *Porter 220, 222* (CAS, DS); 11 mi. S Mulegé, *Porter 227* (CAS, DS); Isla San Marcos, *Ferris 8640* (DS); Isla Coronados, *Moran 3904* (DS); Isla Cedros, *Haines & Hale*, 17 Feb. 1939 (CAS, DS, UC), *Stewart 41* (CAS); Isla Natividad, *Stewart 78-79* (CAS).

The following specimens were probably collected somewhere in northeastern Baja California within the confines of the Lower Colorado Valley, the data on the labels notwithstanding: Tijuana, *Orcutt & Orcutt*, 30 June 1884 (GH, NY, UC); Valle de las Palmas, *Jones 3691* (CAS, DS, NY, UC); Ensenada, *Jones, 1882* (GH). These localities are well within the more mesic Californian Region, and other collections of *Fagonia* are unknown from this area.

Fagonia laevis, the most common *Fagonia* in Baja California, is found from the International Boundary south to an approximate latitude of 26° N, where it extends slightly into the range of *F. californica*. It also occurs in the Mojave Desert and is found northward into the Great Basin Desert. It is known from southwestern Arizona south to the vicinity of Guaymas, Sonora. This species is commonly encountered in abundance in rocky and hilly surroundings, being more rarely found on sandy plains. It occurs in both granitic and volcanic soils.

Fagonia longipes Standl., from the Lower Colorado Valley subdivision of the Sonoran Desert in southwestern Arizona and southeastern California, has long been considered a synonym of *F. laevis*. However, *F. longipes* is a distinct taxon, separable from *F. laevis* by its long pedicels, glandular-stipitate branches, pedicels, petioles, and leaflets, and its glandular fruits. *Fagonia longipes* differs from *F. californica* in its slender growth, longer pedicels and petioles, and linear leaflets. This species is not known from Baja California.

5. **Fagonia villosa** D. M. Porter, sp. nov.

Prostrate-spreading; herbage densely to sparingly villous, hairs with thickened bases and appressed toward the branch apices, older parts becoming glabrate and occasionally scabrous; stipules reflexed to spreading, subulate, 1-6 mm. long; leaflets 3, ovate or obovate to elliptic (rarely linear), apical leaflet 1-8.5 mm. wide and 2-23 mm. long, lateral leaflets to 4 mm. wide and 16 mm. long; petioles 1-10 (rarely to 15) mm. long; flowers to ca. 1 cm. in diameter; pedicels 1-7 (rarely to 9) mm. long; sepals linear-oblong, villous, green to purple, 1-1.5 mm. wide, 2-4 mm. long; petals pink to red-purple (rarely white), 1-3 mm. wide, 4-6 mm. long; filaments 3-4 mm. long; ovary pubescent, style 1-2 mm. long; fruiting pedicels 1-6 (rarely to 10) mm. long; fruit puberulent, 3.5-6 mm. wide, 3.5-4.5 mm. high; beak 1-2 mm. long; seeds 1-2 per locule.

Planta patuli-prostrata, dense vel sparse villosa, pili ad basem incrassati, apices ramulorum versus appressi, partes vetustiores glabratae vel aliquando scabrae; stipulae reflexae vel patulae, subulatae, 1-6 mm. longae; foliola 3, ovata, obovata, vel elliptica (raro linearia), foliolum apicale 1-8.5 mm. latum et 2-23 mm. longum, foliola lateralia ad 4 mm. lata et 16 mm. longa; petioli 1-10 mm. longi (raro 15 mm.); flores ad 1 cm. diam.; pedicelli 1-7 mm. longi (raro 9 mm.); sepala lineari-oblonga, villosa, viridia vel purpurea, 1-1.5 mm. lata, 2-4 mm. longa; petala rosea vel rubropurpurea (raro alba), 1-3 mm. lata, 4-6 mm. longa; filamenta 3-4 mm. longa; ovarium pubescens, stylus 1-2 mm. longus; pedicelli fructiferi 1-6 mm. longi (raro 10 mm.); fructus puberulus, 3.5-6 mm. latus, 3.5-4.5 mm. altus; rostrum 1-2 mm. longum; semina 1-2 in loculo.

TYPE: *Porter 426*, collected 8 March 1960 at "Roadside on gently sloping hill on old highway W of La Paz, 10.5 miles W of junction with new highway. Common. Flowers rose-purple, few in flower. Some prostrate-spreading; others rather upright, bushy." The holotype is deposited in the Dudley Herbarium of Stanford University (no. 445,587). Isotypes are deposited in the Herbarium of the California Academy of Sciences; Herbario Nacional del Instituto de Biología de la Universidad Nacional de México; Conservatoire et Jardin Botaniques, Geneva; Herbarium of the University of California, Berkeley; Herbarium of the University of Arizona, Tucson; Herbarium of the University of Texas, Austin; and the United States National Museum, Smithsonian Institution.

SPECIMENS EXAMINED: 40 mi. E El Rosario, *Wiggins 4476* (DS, GH); Lagoon Head, *Palmer 827* (CAS, GH, NY); 12 mi. S El Solito, *Wiggins 15139* (CAS, DS); 12 mi. NW Guadalupe, *Porter 535* (CAS, DS); 0.5 mi. NW Guadalupe, *Porter 531, 532* (CAS, DS); 7 mi. S Los Angeles, *Wiggins & Ernst 628* (CAS, DS); El Carrizal, *Porter 506* (CAS, DS); 8 mi. N San Juanico, *Gentry 4307* (DS, GH, UC); 1 mi. N San Juanico, *Porter 504* (CAS, DS); Arroyo de Mezquital, *Porter 502* (CAS, DS); 18 mi. NW road to Comondú toward La Purísima, *Porter 494* (CAS, DS); 0.75 mi. NW road to Comondú toward La Purísima, *Porter 491* (CAS, DS); 25.5 mi. SW San José Comondú, *Porter 234* (CAS, DS); 51 mi. N El Crucero, *Porter 487* (CAS, DS); 8 mi. N Santo Domingo, *Thomas 8386* (DS); 30 mi. NW El Crucero, *Porter 486* (CAS, DS): 24 mi. NW El Crucero, *Porter 484* (CAS, DS); S El Refugio, *Wiggins 5525* (DS, UC); 9.5 mi. S El Refugio, *Porter 460* (CAS, DS); 11 mi. NW Santa Rita toward

Llanos de Hiray, *Porter 470* (CAS, DS); 8.5 mi. NW Santa Rita toward Llanos de Hiray, *Porter 471* (CAS, DS); 4 mi. inland from Puerto Chale, *Chambers 813* (DS, UC); 58.5 mi. NW La Paz, *Porter 475* (CAS, DS); 52.5 mi. NW La Paz, *Porter 443* (CAS, DS); 46.5 mi. NW La Paz, *Porter 441* (CAS, DS); 42.5 mi. NW La Paz, *Porter 439* (CAS, DS); 19 mi. W km. 38.5 on main highway W La Paz, *Porter 435* (CAS, DS); 15.5 mi. W km. 38.5, *Porter 431* (CAS, DS); 2 mi. N Arroyo Seco, *Porter 430* (CAS, DS); 22.5 mi. W new highway toward Arroyo Seco, *Porter 429* (CAS, DS); 14.5 mi. W new highway toward Arroyo Seco, *Porter 428* (CAS, DS); Todos Santos, *Jones 24092* (CAS, DS, NY, UC); 3 mi. S Todos Santos, *Porter 371, 371A* (CAS, DS); San José del Cabo, *Brandegee 81* (DS, UC).

This plant has long gone under the name *Fagonia californica* var. *barclayana* Benth. but a careful examination of the holotype of that taxon reveals that is has short straight hairs, stipitate glands, and glandular fruits, not the appressed villous hairs and glandless fruits of *F. villosa*. *F. californica* var. *barclayana* is, therefore, now applied to what has been hitherto known as *Fagonia insularis* Standl. I have chosen to name this species *Fagonia villosa* because of the prominent pubescence, which differs from that of any other North American *Fagonia*.

This is the most common species of *Fagonia* in the southern half of Baja California. It is known to occur along the western side of the peninsula from near El Rosario to San José del Cabo. It is most common from the southern end of the Magdalena Plain and northward across the Vizcaíno Desert; it has been collected sparingly north and south of this range.

Fagonia villosa is a plant of flat sandy areas or of sandy arroyo margins, but it is occasionally collected in rocky soils.

Flowers of *Fagonia villosa* are usually pink to red-purple, but white-flowered individuals are rarely found (*Porter 531* and *Wiggins 5525*). These may or may not occur within populations containing the normal flower color.

6. **Fagonia pachyacantha** Rydb. in Vail & Rydb., N. Amer. Fl. 25:105. 1910

Fagonia californica var. *glutinosa* Pringle ex Vail, Bull. Torr. Bot. Club. 22:229. 1895. Not *F. glutinosa* Del., 1813.

Fagonia viscosa Rydb. in Vail & Rydb., N. Amer. Fl. 25:104. 1910. Not *F. viscosa* Hochst. ex Boiss., 1867.

Fagonia chilensis var. *glutinosa* (Pringle ex Vail) Johnst. Proc. Calif. Acad., ser. 4, 12:1051. 1924.

Fagonia chilensis var. *pachyacantha* (Rydb. in Vail & Rydb.) Johnst., *loc. cit.*

Fagonia californica ssp. *pachyacantha* (Rydb. in Vail & Rydb.) Wiggins, Contr. Dudley Herb. 4:19. 1950.

Prostrate-spreading, to 4 ft. in diameter; ultimate branches thickly beset with large short-stipitate to subsessile globular (drying to cup-shaped) golden glands, older parts glabrate; ultimate branches usually appearing yellowish from a distance because of the many glands; stipules stout, linear-subulate, spreading to slightly reflexed, glandular to glabrate, 3-16 mm. long; leaflets 3, ovate to elliptic, slightly obovate, or linear and terete, glandular, becoming glabrate, apical leaflet to 10 mm. wide and 1-26 mm. long, lateral leaflets to 7 mm. wide and 1-20 mm. long, one or both laterals commonly caducous; petioles glandular to glabrate, 2-16 mm. long; flowers to ca. 1.5 cm. in diameter; pedicels glandular, 1-7 mm. long; sepals oval, glandular to glabrate, green to purple, 1-1.5 mm. wide, 2-2.5 mm. long; petals light to dark red-purple, 2.5-5.5 mm. wide, 5-8 mm. long; filaments 3.5-5 mm. long; ovary pubescent and glandular, style 2-2.5 mm. long; fruiting pedicels glandular, 1-6 mm. long; fruit puberulent and glandular, 4-5 mm. wide, 3.5-4 mm. high; beak 1.5-3.5 mm. long; seeds 1 per locule. Flowering and fruiting from February to May.

TYPE LOCALITY: "Type collected in Baja California (date and exact locality not given), *Leon Diguet* (herb. N. Y. Bot. Gard.)." (Vail & Rydberg, 1910, p. 105).

SPECIMENS EXAMINED: Baja California, *Diguet s. n.* (NY!; type fragment at UC); 24 mi. W Mexicali, *Porter 619* (CAS, DS); 5 mi. S La Ventana, *Wiggins 15765* (CAS, DS); 9 mi. N San Felipe, *Porter 617* (CAS, DS); 2.7 mi. N San Felipe, *Raven 14768* (DS); 18 mi. S San Felipe, *Wiggins 15817* (CAS, DS); 13.5 mi. N Puertecitos, *Porter 615* (CAS, DS); 15 mi. S Puertecitos, *Porter 612* (CAS, DS); 72 mi. S San Felipe, *Wiggins & Ernst 683* (CAS, DS); 26.5 mi. S Puertecitos, *Porter 607* (CAS, DS); 35 mi. S Puertecitos, *Porter 606* (CAS, DS); 15 mi. N Bahía de San Luis Gonzaga, *Wiggins 16040* (CAS, DS); 4 mi. N Bahía de San Luis Gonzaga, *Wiggins 16035* (CAS. DS); 19.5 mi. N Las Arrastras, *Porter 604* (CAS, DS); 11.5 mi. NW Calamajué, *Porter 600* (CAS. DS); 3.5 mi. NW Calamajué, *Porter 597* (CAS, DS); 7.5 mi. N turnoff to Calamajué 24 mi. N Punta Prieta, *Porter 588* (CAS, DS); 4.1 mi. NW Bahía de los Angeles, *Porter 181* (CAS, DS), *181A* (DS); 3.5 mi NW Bahía de los Angeles, *Porter 575* (CAS, DS); Bahía de los Angeles. *Palmer 546* (GH, NY); 2.5 mi. S village at Bahía de los Angeles, *Porter 566* (CAS, DS); SE part Bahía de los Angeles, *Porter 571* (CAS, DS); Bahía de San Francisquito, *Johnston 3555* (CAS, GH); Santa Rosalía, *Palmer 180* (GH, NY); 1 mi. S Santa Rosalía, *Porter 218* (CAS, DS); 7 mi. S Santa Rosalía, *Porter 219, 221* (CAS, DS); Isla Angel de la Guarda, *Johnston 3385* (CAS, GH).

Fagonia pachyacantha is easily recognized by its prostrate-spreading, open habit, and its large golden short-stipitate to subsessile glands. This species occurs in sandy washes, on rocky hillsides, and on flat plains. It is found in both granitic and volcanic soils along the Gulf Coast of Baja California from the International Boundary to a few miles south of Santa Rosalía. It occurs northward into southeastern California, southwestern Arizona, and northwestern Sonora, all within the Lower Colorado Valley subdivision of the Sonoran Desert.

Fagonia pachyacantha is found almost entirely within the range of *F. laevis*, but there appears to be partial ecological isolation between them. *F. pachyacantha* tends to be a plant of flat, sandy areas, while *F. laevis* is more apt to be found in rocky, hilly surroundings.

7. **Fagonia barclayana** (Benth.) Rydb. in Vail & Rydb., N. Amer. Fl. 25:104. 1910

Fagonia californica var. *barclayana* Benth., Bot. Sulph. 10. 1844.

Fagonia insularis Standl., Proc. Biol. Soc. Wash. **24**:247. 1911.

Fagonia chilensis var. *barclayana* (Benth.) Johnst. Proc. Calif. Acad., ser. 4. **12**:1051. 1924.

Fagonia chilensis var. *insularis* (Standl.) Johnst., *loc. cit.*

Fagonia californica ssp. *insularis* (Standl.) Wiggins, Contr. Dudley Herb. **4**:19. 1950.

Prostrate-spreading, to 4 ft. in diameter; herbage on younger parts densely covered with small stipitate glands and with occasional small straight hairs, older parts densely pubescent with small straight hairs (becoming less glandular and more pubescent with age), oldest parts becoming glabrous and occasionally scabrous; stipules stout, linear-subulate, spreading, 3-9 mm. long; leaflets 3, linear to broadly ovate, glandular and pubescent, apical leaflet to 19 mm. wide and 28 mm. long, lateral leaflets to 10 mm. wide and 20 mm. long; petioles 3-15 mm. long; flowers to ca. 1.5 cm. in diameter; pedicels glandular and pubescent, 3-14 mm. long; sepals ovate, glandular, green to purple, 1.5-2 mm. wide, 2.5-4 mm. long; petals rose to purple, 2.5-5.5 mm. wide, 5-9 mm. long; filaments 4-6 mm. long; ovary pubescent and glandular, style 2.5-4 mm. long; fruiting pedicels glandular and pubescent, 3-12 mm. long; fruits densely glandular and sparingly puberulent, 4-6 mm. wide, 3-5 mm. high; beak 2-4 mm. long; seeds 1 per locule.

Flowering and fruiting from November to June.

TYPE LOCALITY: "Magdalena Bay" (Bentham, 1844, p. 10).

SPECIMENS EXAMINED: Bahía Concepción, *Shreve 7093* (DS, GH); Punta Guadalupe, *Johnston 4155* (CAS, GH, NY, UC); 19 mi. S Mulegé, *Porter 229* (CAS, DS); 20 mi. S Mulegé, *Wiggins 11411A* (DS); 54.5 mi. S Mulegé, *Porter 231* (CAS, DS); 6 mi. W Canipolé, *Wiggins 11447* (DS, GH, UC); 2 km. NE San Isidro, *Moran 7463* (DS); La Purísima, *Gentry 4216* (DS, GH, UC); 10 mi. W Comondú, *Gentry 4091* (DS); 15.5 mi. SW San José Comondú, *Porter 232* (CAS, DS); Bahía Magdalena, *Barclay s. n.* (K!); 1 mi. S Missión Los Dolores landing, *Wiggins, Carter, & Ernst 238* (CAS, DS, UC); 13 mi. N El Pilar, *Wiggins 15462* (CAS, DS);

Bahía de los Muertos, *Wiggins 14444A* (DS); Isla Coronados, *Johnston 3767* (CAS); Isla Carmen, *Johnston 3806* (CAS), *Palmer 830* (US), *Wosnessensky*, 2 Feb. 1842 (GH); Isla Danzante, *Moran 9239* (GH); Isla Monserrate, *Moran 3892* (DS, UC), *Rose 16604* (NY); Isla San José, *Moran 3786* (DS, UC); Isla San Francisco, *Johnston 3958* (CAS), *Moran 3709* (DS), *Wiggins, Carter, & Ernst 395* (CAS, DS, UC).

This taxon previously has been known under the name *Fagonia insularis* Standl.; however, an examination of the holotypes of North American *Fagonia* reveals that *F. insularis* is in reality a synonym of *F. barclayana*. The plants hitherto known under the name *F. californica* var. *barclayana* are now referred to *F. villosa, q. v.*

This prostrate species is found in rocky canyons and on rocky hillsides from the vicinity of Bahía de la Concepción south to Bahía de los Muertos, being found mainly on the eastern side of the peninsula. *Fagonia barclayana* occurs on the islands in the Gulf of California from Isla Carmen south to Isla San Francisquito and is also known from near Guaymas, Sonora.

The collection of *F. barclayana* from Bahía de los Muertos approaches *F. californica* in its overall appearance, but it has the typical pubescence of *Fagonia barclayana.*

5. **Tribulus** L., Sp. Pl. 1:386. 1753

Prostrate to suberect herbs, annual or from a perennial rootstock; diffusely branching, branches striate, green, becoming yellow, to several meters long; herbage more or less sericeous or appressed-villous and somewhat hispid, youngest parts and nodes more densely so, oldest parts becoming glabrate. Stipules subulate to lanceolate, green to somewhat membranaceous, pubescent. Leaves opposite, even-pinnate, one alternate leaf smaller than the other or aborting, dark green; leaflets 3-7 pairs, petiolulate, oblong to elliptic or slightly ovate, mucronate, inequilateral, base oblique, lower surface densely sericeous, upper surface (especially along midvein) less so to glabrate; rachis densely appressed-villous and hispid, a slender green mucro 1-2 mm. long at the apex between the ultimate leaflets. Flowers solitary, pedicels appressed villous and hispid, in the axils of the alternately smaller leaves. Sepals 5, ovate to lanceolate, pubescent, edges membranaceous, deciduous. Petals 5, yellow (rarely white), obovate, apex rounded to slightly lobed. Stamens 10, inserted on the 10-lobed disc, the 5 opposite the petals exterior and usually slightly longer, adnate to the bases of the petals, the 5 opposite the sepals subtended by a small exterior gland, occasionally sterile; filaments linear-subulate; anthers sagittate, sub-basifixed. Ovary sessile or essentially so, 5-lobed, 5-loculed, ovoid, densely hirsute-pilose, the appressed white hairs totally obscuring it; ovules 3-5 per locule, placentation axile; style 1-4 mm. long, stout to cylindrical; stigma globose, 5-lobed, ca. 1 mm. in diameter. Fruiting pedicels appressed-villous, hispid, terminally reflexed downward; the horizontally flattened fruit consisting of 5 indehiscent nutlets (rarely 1 or more aborting), each with 2-4 stout spines, occasional smaller spines, and aristate tubercles on the dorsal surface; nutlets hispid at the base, inner faces reticulate, leaving no central axis when falling, divided internally by oblique transverse septa into 3-5 1-seeded locules. Seeds oblong, covered with a white aril, ca. 3 mm. long and 1 mm. in diameter, completely filling the locules.

TYPE SPECIES: *Tribulus terrestris* L.

This genus has its center of distribution in the Mediterranean region, where members are mainly plants of the open desert. Many species have been described from this area, but most of these are undoubtedly synonyms of the ubiquitous *Tribulus terrestris*. Two species are known from Baja California, one introduced, the other probably a native.

KEY TO THE SPECIES

Plants annual; prostrate; leaves to 45 mm. long; leaflets 4-6 pairs; flowers ca. 5 mm. in diameter; pedicels usually shorter than the leaves .... 1. *T. terrestris*.

Plants perennial; prostrate to suberect; leaves to 75 mm. long; leaflets 5-7 pairs; flowers to ca. 4 cm. in diameter; pedicels usually longer than the leaves .... 2. *T. cistoides*.

1. **Tribulus terrestris** L., Sp. Pl. **1**:387. 1753

Prostrate annual, branches radiating from the root to a length of 3 m.; stipules 1-5 mm. long, to 1 mm. wide; leaves 10-45 mm. long, usually longer than the pedicels; leaflets 4-6 (rarely 3) pairs, oblong to slightly ovate, 1-4 mm. wide, 4-11 mm. long; flowers to ca. 5 mm. in diameter; pedicels 2-7 mm. long; sepals ovate, 1.5-2 mm. wide, 2-3 mm. long; petals bright yellow, occasionally lighter at the bases, 2-3 mm. wide, 3-5 mm. long; filaments ca. 2 mm. long, anthers ca. 0.5 mm. in diameter; style stout, ca. 1 mm. long; fruiting pedicels 5-15 mm. long; fruits to ca. 1 cm. in diameter, excluding spines; nutlets ca. 5 mm. high, the 2 large spines 4-7 mm. long, spines puberulent to almost glabrate (more so than the rest of the nutlet), occasionally with a few smaller spines, these 1-2 mm. long and recurved.

The following chromosome numbers have been reported for this species: $n = 12$ (Sugiura, 1940); $2n = 24$ (Negodi, 1939; Heiser and Whitaker, 1948) $2n = 48$ (Schnack and Covas, 1947).

TYPE LOCALITY: "Habitat in Europa australi ad semitas" (Linnaeus, 1753, p. 387).

The determination of the full synonomy of this species is at present almost an impossibility. The genus *Tribulus* is in need of revision, preferably with the aid of cytotaxonomic methods.

SPECIMENS EXAMINED: El Crucero, *Porter 483* (CAS, DS); 46.5 mi. W La Paz, *Porter 442* (CAS, DS); 36 mi. W La Paz, *Porter 445* (CAS, DS); 22 mi. W La Paz, *Porter 474* (CAS, DS); Los Aripes, *Porter 420* (DS);

1.5 mi. W La Paz, *Wiggins 15714* (CAS, DS, GH); 1 mi. W La Paz, *Porter 355* (CAS, DS); La Paz, *Thomas 7803* (DS); 6.5 mi. N La Paz, *Porter 405* (CAS, DS); Rancho El Ciprés, 8 mi. NE La Paz, *Porter 373, 373A* (CAS, DS); 1.5 mi. S La Paz airport, *Porter 372* (CAS, DS); Todos Santos, *Porter 343* (CAS, DS).

Tribulus terrestris has been collected in the Cape Region of Baja California, but it is probably more common throughout the peninsula than present collections would indicate. Johnson (1958, p. 222) reports finding the plant in the northwest "on the dunes at the deserted town of San Quintín." The species also surely occurs in the northeast near Mexicali, but I have seen no specimens from that area, which is immediately south of the heavily infested Imperial Valley of California. Wherever I have seen *Tribulus terrestris* in Baja California, it has been extremely common. This was the situation both at El Pescadero and San José del Cabo.

This noxious weed has undoubtedly invaded Baja California both from the south through the Cape Region, where it may have been introduced with ships' ballast or livestock, and from the north through California, where it was first collected at Santa Monica in 1902 (Davidson and Moxley, 1923). *Tribulus terrestris* has long been a serious agricultural pest in the Central Valley of California, but there is no evidence that it has yet become so in Baja California.

2. **Tribulus cistoides** L., Sp. Pl. 1:387. 1753

Kallstroemia cistoides (L.) Endl., Ann. Naturg. Mus. Wien, 1:184. 1836.

Tribulus terrestris var. *cistoides* (L.) Oliver, Fl. Trop. Africa, 1:284. 1868.

Prostrate to suberect perennial; stipules 3-9 mm. long, 1-5 mm. wide; leaves 15 to 75 mm. long, usually shorter than the fruiting pedicels; leaflets 5-7 pairs, oblong to elliptic, 4-8 mm. wide, 10-19 mm. long; flowers to ca. 4 cm. in diameter; pedicels 8-40 mm. long; sepals lanceolate, 2-3 mm. wide, 6-9 mm. long; petals bright yellow, 5-16 mm. wide, 8-22 mm. long; filaments 4-6 mm. long, anthers ca. 2 mm. long; style cylindrical, 3-4 mm. long; fruiting pedicels 20-45 mm. long; fruits to ca. 1.5 cm. in diameter, excluding spines; nutlets ca. 10 mm. high, the 4 large spines 5-8 mm. long, more densely hispid than in the former species.

TYPE LOCALITY: "Habitat in America calidiore" (Linnaeus, 1753, p. 387).

SPECIMEN EXAMINED: San José del Cabo, *Porter 326* (CAS, DS).

This large-flowered *Tribulus* is primarily a plant of the coastal strand, especially common in the New World tropics and the Southwest Pacific, where it is apparently indigenous. *T. cistoides* is known to occur from Florida to Texas and Georgia in the southeastern United States (Small, 1933), and there is a collection of the plant in the Herbarium of the California Academy of Sciences (*Skoss*, 7 May 1948) labeled, "Kern River Valley 7 Miles below Hobo Hot Springs, Kern County [California]." This specimen is the only one of which I am aware from the western United States.

Tribulus cistoides has been collected in Baja California only at San José del Cabo, where it is quite common, sometimes growing side by side with *T. terrestris*. According to Ira L. Wiggins (personal communication), the species is also abundant at the La Paz airport. Vail (1895) lists *T. cistoides* as occurring in Baja California, but I have seen no specimens from the peninsula other than my own.

6. **Kallstroemia** Scop., Introd. 212. 1777

Prostrate to suberect annual herbs; diffusely branching, branches decumbent, striate, green, becoming yellow, to a meter or more in length; herbage pubescent, youngest parts and nodes more densely so, oldest parts occasionally glabrate. Stipules subulate to lanceolate, green to somewhat membranaceous, pubescent. Leaves opposite, even-pinnate, one alternate leaf smaller than the other or aborting, light to dark green. Leaflets 2-6 pairs, petiolulate, oblong to elliptic, usually mucronate, inequilateral, base oblique, the terminal pair usually broader and shorter than the others, more or less pubescent; rachis densely appressed villous and hispid, a small green mucro at the apex between the ultimate leaflets. Flowers solitary; pedicels in the axils of the alternately smaller leaves, pubescent, thickened upward, longer or shorter than the subtending leaves. Sepals 5-6, lanceolate to subulate, densely pubescent, marcescent, persistent to deciduous. Petals 4-6, orange to yellow or occasionally white, obovate, apex rounded to slightly lobed. Stamens 8-12, those opposite the petals exterior and usually slightly longer, adnate to the bases of the petals, those opposite the sepals subtended by a small exterior gland, occasionally sterile; filaments filiform to subulate; anthers rounded to oblong, sagittate, sub-basifixed. Ovary sessile or essentially so, 8-12-lobed, 8-12-loculed, ovoid, densely tomentose; ovules 1 per locule, placentation axile; style to 8 mm. long, cylindrical; stigmatic areas radiating downward from the tip of the style, vertically grooved. Fruiting pedicels pubescent, usually thickened upward, occasionally markedly so. Fruit ovoid, 8-12-angled, muricate, 4-5 mm. in diameter, separating at maturity into 8-12 indehiscent nutlets; nutlets puberulent, dorsally tuberculate, spineless, more or less reticulate on the inner faces, 1-seeded, falling away from the persistent styliferous axis. Seeds obovate, completely filling the locules.

TYPE SPECIES: *Tribulus maximus* L.

Kallstroemia is a genus of a dozen or so species found in the more arid tropics and subtropics of the New World. It occurs from the southern borders of the United States to Brazil and Argentina, but members are most common in Mexico and the West Indies. The genus was originally included in *Tribulus* and has from time to time been reassigned there by a few botanists. However, the fruits and their development are of sufficient distinctness to warrant the separation of the two genera.

KEY TO THE SPECIES

Plants prostrate to suberect; leaves 15-65 mm. long; pedicels longer than the subtending leaves; petals 12-20 mm. long; beak of the fruit 5-10 mm. long .... 1. *K. grandiflora.*

Plants prostrate; leaves 5-40 mm. long; pedicels shorter than the subtending leaves; petals 3-12 mm. long; beak of the fruit 1-7 mm. long

- Petals 6-12 mm. long; sepals 5-8 mm. long; beak of the fruit cylindrical from a conical base, 4-7 mm. long .... 2. *K. parviflora.*
- Petals 3-6 mm. long; sepals 2-4 mm. long; beak of the fruit conical, 1-3 mm. long .... 3. *K. californica.*

1. **Kallstroemia grandiflora** Torr. ex Gray, Pl. Wright. 1:28. 1852

Kallstroemia grandiflora var. *detonsa* Gray, *loc. cit.*

Tribulus grandiflorus (Torr. ex Gray) Benth. & Hook. ex Brew. & Wats., Bot. Calif. 1:91. 1876.

Tribulus fisheri Kell. Proc. Calif. Acad. 7:162. 1877.

Kallstroemia grandiflora var. *arizonica* Cockerell, Bull. Torr. Bot. Club 27:87. 1900.

Prostrate to suberect; herbage hispid and appressed-villous or sericeous; stipules subulate to lanceolate, 1-2 mm. wide, 2-7 mm. long; leaves 15-65 mm. long; leaflets 2-5 pairs, elliptic to oblong, both surfaces sericeous and appressed-villous, underside more so, 5-12 mm. wide and 10-22 mm. long; pedicels usually longer than the subtending leaves, 10-55 mm. long; sepals lanceolate, 1-2 mm. wide, 6-10 mm. long, surpassing the fruit, but shorter than the style, persistent; petals orange, occasionally turning white with age, 7-14 mm. wide, 12-20 mm. long, apex broadly rounded; filaments subulate, 4-9 mm. long; anthers 1-3 mm. long; ovary 2-3 mm. in diameter; style 6-8 mm. long; stigmatic areas extending along the upper half of the style; fruiting pedicels 15-65 mm. long; fruits to 5 mm. in diameter; nutlets with rounded tuberculae, 3 mm. high; beak of the fruit cylindrical, hardly thickened at the base, 5-10 mm. long.

In Baja California flowering from August to March and fruiting from September to March.

TYPE LOCALITY: "Borders of the Gila [Arizona], *Col Emory*" (Gray, 1852, p. 28).

SPECIMENS EXAMINED: 95 km. NW La Paz, *Wiggins 15413* (CAS, DS); 24 mi. W La Paz, *Porter 438* (DS); Arroyo Seco, *Hammerly 189* (CAS, DS); 15 mi. W La Paz, *Hammerly 222* (CAS, DS); 10 mi. SE La Paz toward Los Planes, *Wiggins 15686* (CAS, DS); 1 mi. S San Antonio toward Santiago, *Chambers 860* (DS, UC); 12.8 km. N Santiago, *Carter, Alexander, & Kellogg 2181* (DS); Los Frailes, *Porter 318* (CAS, DS); Arroyo Salado, *Purpus 409* (UC);San José del Cabo, *Brandegee 78* (UC), *Brandegee*, 5 Sept. 1891 (DS); 3 mi. NE San Lucas, *Porter 331* (CAS, DS); 14 mi. N San Lucas, *Porter 341* (CAS, DS).

Kallstroemia grandiflora occurs from southern California east to Texas and south to Michoacán. Vail (1895) states that it is found south to Guatemala, but I have seen no specimens from that far south, nor have I seen any other references to substantiate her statement. In Baja California this plant is found in the Cape Region and the southern part of the Magdalena Region. It is mainly a plant of low sandy areas and beaches, but Johnson (1958) states that she saw it at a height of between 3500 and 4500 feet in the Sierra Laguna.

Brewer and Watson (in Brewer, Watson, & Gray, 1876) erroneously cite the combination "*T. grandiflorus* Benth. & Hook.", giving the source as "Gen. Pl. i. 264." Bentham and Hooker, however, never made this combination; they simply listed *Kallstroemia* as a synonym for *Tribulus*.

2. **Kallstroemia parviflora** Nort., Ann. Rep. Mo. Bot. Gard. 9:153. 1898

Kallstroemia laetevirens Thornb. in Woot. & Standl., Contr. U. S. Nat. Herb. **16**:143. 1913.

Prostrate; herbage densely to sparingly hispid and villous or sericeous; stipules lanceolate, 1-1.5 mm. wide, 5-7 mm. long; leaves to 40 mm. long; leaflets 3-5 pairs, oblong, sericeous, underside more so than upper, 3-6 mm. wide, 6-13 mm. long; pedicels shorter than the subtending leaves, 10-20 mm. long; sepals subulate to lanceolate, to 1.5 mm. wide, 5-8 mm. long, more or less persistent; petals yellow to orange, 3.5-9 mm. wide, 6-12 mm. long; filaments linear-subulate, 3-6 mm. long; ovary 1-2 mm. in diameter; style 3-4 mm. long; fruiting pedicels 14-45 mm. long; fruits 4-5 mm. in diameter; nutlets with rounded tuberculae, 3-4 mm. high; beak of the fruit cylindrical, thickened at the base, 4-7 mm. long.

Known to flower and fruit in Baja California from October to January.

TYPE LOCALITY: "Collected at Agricultural College, Miss., by Pollard, Aug., 1896, no. 1295" (Norton, 1898, p. 153).

SPECIMENS EXAMINED: Near km. 40 on main highway NW La Paz, *Thomas 8439* (DS, GH); 15.5 mi. SE La Paz toward Las Cruces, *Wiggins 15669A* (CAS, DS); near fork of road toward Punta Arena, *Wiggins 14454* (CAS, DS); 3 km. N Cabo San Lucas, *Moran 7040* (CAS, DS).

Kallstroemia parviflora is found from southern California east to Mississippi and south to Michoacán, in Mexico. It occurs sparingly in the Cape Region of Baja California.

With the exception of *Thomas 8439*, all the specimens examined approach *Kallstroemia grandiflora* in petal size, but their other characters indicate that they are in all probability large-flowered examples of *K. parviflora*.

3. **Kallstroemia californica** (S. Wats.) Vail. Bull. Torr. Bot. Club **22**:230. 1895

Tribulus californicus S. Wats., Proc. Amer. Acad. **11**:125. 1876.

KEY TO THE VARIETIES

Leaflets 3-6 pairs, to 3 mm. wide and 7 mm. long; petals 1-2 mm. wide, 3-5 mm. long; beak of the fruit 1-2 mm. long; nutlets sharply tuberculate .... 3a. *K. californica* var. *californica*.

Leaflets 2-4 pairs, 3-10 mm. wide, 6-21 mm. long; petals 2-3 mm. wide, 4-6 mm. long; beak of the fruit 2-3 mm. long; nutlets rounded tuberculate .... 3b. *K. californica* var. *brachystylis*.

3a. **K. californica** var. **californica**

Prostrate; herbage hispid and appressed-villous or sericeous; stipules subulate, to 1.5 mm. wide, 2-3 mm. long; leaves 5-35 mm. long; leaflets 3-6 pairs, elliptic, sericeous, especially on underside, becoming almost glabrate, to 3 mm. wide and 7 mm. long; pedicels shorter than the subtending leaves, 2.5-10 mm. long; sepals lanceolate, to 1 mm. wide, 2-3 mm. long, deciduous; petals cream to yellow, 1-2 mm. wide, 3-5 mm. long; filaments filiform, 2 mm. long; ovary ca. 1 mm. in diameter; style to 1 mm. long; fruiting pedicels 4-26 mm. long; fruits 5 mm. in diameter; nutlets sharply tuberculate, 3 mm. high, the 4 or 5 tuberculae to 1 mm. long; beak of the fruit thick, conical, glabrous, 1-1.5 mm. long.

Flowering and fruiting in September and October in Baja California.

TYPE LOCALITY: "Collected by Dr. E. Palmer, in Lower California (1870), on the eastern side of the peninsula" (Watson, 1876, p. 125). According to McVaugh (1956), in 1870 Edward Palmer collected in Baja California at and near La Paz (5 January) and Cabo San Lucas (9 January and 7 February) and on Isla Carmen (1 January). He may also have been at the mouth of the Colorado River in late August or early September of that year.

SPECIMENS EXAMINED: Lower California, *Palmer, 1870* (GH!); 1.5

mi. SW Los Mártires, *Thomas 8317* (DS); San José del Cabo, *Brandegee 80* (UC), Sept. 1891 (DS, GH), 28 Sept. 1893 (UC).

Kallstroemia californica var. *californica* is known to occur from southern California and Arizona to Sinaloa. This variety is probably more common in Baja California than the above collections would indicate. It is not nearly so common, however, as *K. californica* var. *brachystylis*, either in Mexico or in the United States.

None of the Baja California collections of this variety has such sharply tuberculate nutlets as specimens from California and Arizona. They do, however, have the many small leaflets that characterize *Kallstroemia californica* var. *californica.*

3b. **K. californica** var. **brachystylis** (Vail) Kearn. & Peeb., Journ. Wash. Acad. **29**:485. 1939

Kallstroemia brachystylis Vail, Bull. Torr. Bot. Club **24**:206. 1897.

Tribulus brachystylis (Vail), Rob. in Gray, Syn. Fl. N. Amer. 1: 354. 1897.

Prostrate; herbage hispid and appressed-villous or sericeous; stipules subulate, to 1 mm. wide, 2-4 mm. long; leaves 5-30 mm. long; leaflets 2-4 pairs, oblong to elliptic, sericeous, more so on underside, to almost glabrate, 3-10 mm. wide, 6-21 mm. long; pedicels shorter than the subtending leaves, 2-20 mm. long; sepals subulate, to 1.5 mm. wide, 2.5-4 mm. long, deciduous; petals cream to orange, 2-3 mm. wide, 4-6 mm. long; filaments filiform, 2-3 mm. long; ovary ca. 2 mm. in diameter; style 1.5-2 mm. long; fruiting pedicels 8-25 mm. long; fruits 4-5 mm. in diameter; nutlets with rounded (rarely a few sharp) tuberculae, 3 mm. high; beak conical, slightly thickened at the base, 2-3 mm. long.

Flowering and fruiting from August to March.

TYPE LOCALITY: "Mesa near Las Cruces, N. M., alt. 3900 ft. Collected by E. O. Wooton, Aug. 12, 1895" (Vail, 1897, p. 206).

SPECIMENS EXAMINED: 15 mi. N Bahía de San Luis Gonzaga, *Wiggins 16037* (CAS, DS); 40 mi. N Laguna Chapala toward San Felipe, *Wiggins & Ernst 679* (CAS, DS); Laguna Chapala, *Thomas 8201* (DS); Bahía de los Angeles, *Wiggins 15002* (CAS, DS); 12 mi. E El Solito, *Wiggins 15144* (CAS, DS); 6 mi. S Rancho Los Angeles, *Wiggins 15166* (CAS, DS); 57 km. NW San Ignacio, *Carter, Alexander, & Kellogg 1951* (DS); between San Ignacio and Los Mártires, *Gentry 7873* (DS, UC); 7 mi. E. San Ignacio, *Wiggins 11355* (CAS, DS, GH, UC); 24 mi. NW Santa Rosalía, *Chambers 979* (DS); 6 mi. NW Cuarenta, *Thomas 8362* (DS, GH); El Coyote, *Hammerly 128* (CAS, DS, GH); 14.4 km. SW Comondú, *Carter, Alexander, & Kellogg 2122* (DS); Rancho del Cayuco, *Carter & Kellogg 3127* (DS), *Jones 27113* (UC); 10 mi. S Missión los Dolores, *Wiggins, Carter & Ernst 322* (CAS, DS, UC); 4.5 km. N Pozo Grande, *Carter, Alexander & Kellogg 2129* (DS); 8.5 mi. N Santo

Domingo toward Pozo Grande, *Thomas 8390* (DS); 18 mi. S El Crucero, *Porter 452* (CAS, DS); 16 mi. S El Refugio, *Wiggins 11495* (DS, UC), *11497* (DS); 3.6 mi. N Punta del Cerro, *Wiggins 15468* (CAS, DS); Rancho Colorado, *Brandegee*, 17 Jan. 1890 (DS, UC), 19 Jan. 1898 (CAS); near km. 40 on main highway NW La Paz, *Thomas 8439A* (DS); 15 mi. W La Paz, *Hammerly 194* (CAS, DS); 8.5 mi. N La Paz, *Porter 384, 384A* (CAS, DS); 8.9 mi. E Los Planes, *Wiggins 14435* (CAS, DS); La Palmilla, *Wiggins 15019* (CAS, DS); San José del Cabo, *Brandegee 79* (UC), 21 Sept. 1891 (GH), 28 Sept. 1893 (UC).

Kallstroemia californica var. *brachystylis* occurs from southern California to Texas and south to Central America. It is found in Baja California in all regions except the Californian. It is by far the most common *Kallstroemia* on the peninsula and occurs mainly on flat sandy areas.

Hammerly 128 and *194* have been elsewhere cited (Johnson, 1958) as *Kallstroemia glabrata* Rydb. This name may prove to be a synonym of *K. californica* var. *brachystylis*.

This variety is often difficult to separate from *Kallstroemia californica* var. *californica*, as there is a distinct overlap between the two in the size of the tubercles. According to Kearney and Peebles (1939, p. 485), "As compared with typical *K. californica*, this form has usually fewer leaflets and shorter, blunter tubercles on the carpels, but there is too much intergradation to warrant specific distinction." Here is another instance in which cytotaxonomic methods would undoubtedly help delimit the differences between entities in this family.

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A TAXONOMIC STUDY OF THE GENUS ANADENANTHERA

SIRI VON REIS ALTSCHUL

The small, tropical to subtropical, and strictly New World genus *Anadenanthera* formerly was considered as section *Niopa* of the genus *Piptadenia* and is the common leguminous source of the so-called narcotics known as *Cohoba, Vilca* and *Yopo.* Because of their unusual effects upon the human nervous system, the chemical constitutents of these materials are of current interest in the field of experimental psychiatry. Among the chemical compounds which have been isolated from the species of *Anadenanthera* may be included some hallucinogenic drugs designated as psychotomimetics (Hofmann, 1959). In contrast to other psychotropic drugs, which merely evoke modifications in the mood of the recipient, the psychotomimetics appear to produce profound and acute changes in perception.

An interest both in plants of possible medical significance and in species in need of taxonomic study provided a stimulus for the research whose results are published in part in this paper. An ethnobotanical treatment which also has been prepared will be published elsewhere. A detailed systematic treatment of the species of *Anadenanthera* has been needed for some time. While additional work still remains to be carried out on this group, as well as on related species in the genus *Piptadenia,* it is hoped that the data presented here from several branches of botany will help better to define *Anadenanthera* and to stimulate further research in the large and relatively neglected subfamily *Mimosoideae.*

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THE GENUS ANADENANTHERA: HISTORY AND THE CHARACTERS OF DISTINCTIVENESS

The species comprising the leguminous genus *Anadenanthera* as here conceived were treated originally as belonging to section *Niopa* of the genus *Piptadenia* Bentham (1840, 1841-42). The species of *Piptadenia* were not well known during Bentham's lifetime, but that author was quick to recognize that a natural distinction could be made between sections *Eupiptadenia* and *Pityrocarpa* with spicate inflorescences, and section *Niopa* with capitate inflorescences. Bentham distinguished five species in section *Niopa*, though he wondered whether they might not better be considered as varieties of a single species. The fruits differed considerably in form and proportion, but the flowers and foliage were very much alike from one specimen to another. Bentham later included four of the original species in his "Revision of the Suborder Mimoseae" of 1874-75: *Piptadenia peregrina* (L.) Bentham, *P. macrocarpa* Bentham, *P. falcata* Bentham and *P. colubrina* (Vell.) Bentham. He placed a fifth species, *P. microphylla* Bentham, in the synonymy of *P. macrocarpa.*

Since Bentham's time, three additional species have been described for section *Niopa* of *Piptadenia. Piptadenia novo-guineensis* Warburg was published first as the monotypic genus *Schleinitzia microphylla* Warburg (1891) and, for reasons discussed in this paper, probably should be returned to its former status. *Piptadenia Hassleriana* Chodat (1904) is referred to synonymy under *Anadenanthera colubrina* var. *Cebil* in the present treatment. *Piptadenia amazonica* Ducke (1915) was recognized by Ducke in 1922 as belonging to *Pithecellobium* Martius (1837).

Piptadenia leptoclada Baker (1887) was based on a specimen with a globose-spicate inflorescence which could be mistaken at first glance for a species intermediate between sections I and II and section III of *Piptadenia sensu* Bentham. The specimen was identified by Perrier de la Bathie in 1938 as *Desmanthus Commersonianus* Baillon (1883).

In 1923, Spegazzini founded the genus *Anadenanthera* to accommodate *Piptadenia peregrina* and *P. falcata.* He based the genus on the flowers' being "without anther glands", a character of doubtful generic value by itself. Spegazzini stated in his description that he did not include in *Anadenanthera* five southern species he had not seen, but which were mentioned in Engler & Prantl (1892). An inspection of those authors' work suggests that Spegazzini must have meant three, not five, other species. For the species named in Engler & Prantl are: *Piptadenia peregrina, P. falcata, P. macrocarpa, P. colubrina* and *P. novo-guineensis.* The last three have anther glands.

In 1927, Britton & Rose proposed to elevate the whole of section *Niopa* to a genus. They offered, however, no reason for the change, added no new information and did not recognize the priority of the name *Anadenanthera.*

In 1955, Brenan proposed a revision of the genus *Pipta-*

denia according to a new set of characters involving, in particular, the mode of dehiscence of the pod and the structure of the seed. The differences he prescribes are comparable to those used elsewhere in the *Mimosoideae* to distinguish genera. Furthermore, they are not infrequently correlated with vegetative differences. Brenan presents fruit and flower keys to eight genera which have species formerly included in *Piptadenia*. These keys delimit groupings which seem to be more satisfactory than have been achieved heretofore. How well some of the genera will be upheld when their species become better known is uncertain, but by conservative judgment, the most natural of them is *Anadenanthera*, which Brenan extends to include all species of former section *Niopa* of *Piptadenia*. He distinguishes *Anadenanthera* by the following combination of characters: the globose inflorescence; the dehiscence of the pod along one suture only; the suborbicular, narrowly or not winged seeds lacking endosperm; and the strictly American distribution.

The evidence available on wood anatomy supports the reasonableness of upholding the genus *Anadenanthera*. Within the *Leguminosae* as a whole, genera of the *Caesalpinioideae* and especially the *Mimosoideae* are noted for a relatively homogeneous wood structure (Cozzo, 1951). Yet Tortorelli indicated preliminarily in 1948 that the element here called *Anadenanthera colubrina* var. *Cebil* is characterized by having incompletely paratracheal parenchyma, with rays three or more cells wide and up to 550 μ high. By comparison, at least two other species of the Piptadenias have wood with definite paratracheal vasicentric parenchyma, rays uniseriate or biseriate and up to 350 μ high: *Piptadenia excelsa* (Grisebach) Lillo (1910) and *P. rigida* Bentham (1842). Recently, Brazier (1958) discovered that differences in wood anatomy within the whole of what now may be referred to as the '*Piptadenia* complex' (Brenan in a letter, October 8, 1959) coincide almost perfectly with the eight generic distinctions proposed by Brenan. Brazier's key to these genera indicates that *Anadenanthera* may be characterized, and distinguished from other genera of the *Piptadenia* complex, by the presence of non-septate fibers and wide, typically (4-)5-seriate rays.

An interest in the Piptadenias on the part of the medical world has led to investigations into the chemical constituents of the reputedly hallucinogenic seeds. This research has shown that the species of *Anadenanthera* are in some ways physiologically different from other species in the *Piptadenia* complex. In 1955, Fish, Johnson & Horning indicated that the seeds of what now are referred to as *Anadenanthera peregrina* var. *peregrina* and *A. colubrina* var. *Cebil* yielded a much larger amount of alkaloid material than was found in *Piptadenia paniculata* Bentham (1842). Fish reported (in a letter, January 7, 1958) a much lower concentration of bufotenine and related substances in three additional species from the *Piptadenia* complex than was found in the seeds of *Anadenanthera peregrina* var. *peregrina* and *A. colubrina* var. *Cebil*. The three species tested were *Piptadenia communis* Bentham (1842), *P. contorta* Bentham (1875) and *P. leptostachya* Bentham (1842).

The information reviewed above, plus the data presented in the pages which follow, require that *Anadenanthera* be recognized as a well substantiated genus of the *Mimosoideae*.

THE SPECIES OF ANADENANTHERA

MATERIALS AND METHODS: This revision is based on herbarium specimens, field work and the literature. Because the fruits still are not known for many species of the *Piptadenia* complex, flowering specimens usually are necessary for identification of material. Over 200 specimens were examined for this study.

The leaflets reproduced in Plates VII-IX and Plate XI were cleared by a technique which is essentially that given by A. S. Foster (1950) for studying foliar venation in angiosperms. The leaflets first were softened in water brought almost to the boiling point. Afterwards, they were soaked in 6% sodium hydroxide for 24-36 hours in an oven at 60 degrees Centigrade. The time required for decolorization varied with the samples. A small, capped vial was used for about a dozen leaflets from each field number. Some of the vials darkened quickly, and the solutions had to be replenished. Leaflets of *Anadenanthera peregrina* var. *falcata*, in particular, released what appeared to be large amounts of pigments or tannins. Differences in decolorizing suggest that a chemical study of the leaflets might uncover facts pertinent to the taxonomy of the genus. When the leaflets had become almost transparent, they were cleared in 85% lactic acid for 10 minutes over a boiling bath. They then were stored in capped bottles of fresh lactic acid for a day or two. The staining was accomplished by bathing the leaflets in distilled water and subsequently in a solution of ¼% safranin and 50% alcohol, for less than 20 minutes. Before becoming too heavily stained, the leaflets were removed, 1-3 to a glass slide. Before they could dry, the leaflets were flooded with successive solutions of 70%, 95% and 100% alcohol and, finally, xylol. A drop of damar was placed under the cover slip. In this study the petals and calyces were not used. They are extremely delicate, nearly clear and finely 1-veined.

DISCUSSION: The genus *Anadenanthera* consists of two species. Each is distinguished by a constellation of a few constant morphological characters and a geographical distribution which is partly overlapping with that of the other species. Specimens can be identified most easily as belonging to either of these two species on the basis of the pod texture. This division correlates with the presence or absence of a minute gland on each anther and with the position of a small involucre surrounding the peduncle. One species, *Anadenanthera peregrina*, has dull, scurfy to verrucose pods, eglandular anthers and the involucre is about three-quarters of the way up the peduncle. It is the more northern-ranging species occurring from southeastern Brazil to the Greater Antilles. The other species, *Anadenanthera colubrina*, has nitid, smooth to reticulated pods, glandular anthers and the involucre just under the receptacle. It is limited to the southern hemisphere and occurs from central Peru to northern Argentina to northeastern Brazil.

Each of the above species may be divided further into two groups of individuals. These groups each can be distinguished by a set of morphological characters correlated with a particular geographical distribution. The differences involved are relative, in that they may appear to be trends when a series of specimens within a species is observed. They also are outstanding enough for representatives in which the characters are fully expressed to have been considered as belonging to separate species. In this treatment, they are regarded as varieties.

PLATE I. Fig. 1. *Anadenanthera peregrina* var. *peregrina* in flower, from Puerto Rico *(P. Sintenis 6706)*. Fig. 2. *Anadenanthera peregrina* var. *peregrina* in fruit, from Venezuela *(Humboldt 1159?, Willdenow Herbarium 19057)*. Fig. 3. *Anadenanthera peregrina* var. *falcata* in fruit, from Brazil *(E. Hemmendorff 285)*. Note the dull pod typical of this species; the falcate shape of the pod, the heavier twigs, and the thicker, fewer leaflets are characteristic of this variety. Fig. 4. *Anadenanthera colubrina* var. *Cebil* in flower, from Bolivia *(J. Steinbach 6657)*.

Anadenanthera peregrina var. **peregrina** (Plate I, figs. 1 & 2) is a tall tree with trunks and branches which are not very corky. The pinna pairs tend to be more numerous but the leaflets fewer, shorter, and straighter than in the other variety, *A. peregrina* var. *falcata.* The leaflets and other vegetative parts of var. *peregrina* generally are thinner. The heads are greener and may be smaller. The legume tends to be longer with a broader range of widths and usually is straight. This variety is found in northern Brazil, British Guiana, Colombia, Venezuela and probably is naturalized where found in the West Indies. Specimens show this to be the more widespread and more northern-ranging variety of *A. peregrina.*

Anadenanthera peregrina var. **falcata** (Plate I, fig. 3) is a much shorter tree with suberose trunks and branches. The leaflets usually are falcate, coriaceous, contrasting dorsiventrally and darker in dried specimens than those of var. *peregrina.* The heads of var. *falcata* are yellowish, and the legume typically is falcate. This variety is found in southern Brazil and Paraguay. Specimens examined show it to be geographically adjacent to var. *peregrina,* representing the southernmost stronghold of the species as a whole.

Anadenanthera colubrina var. **Cebil** (Plate I, fig. 4; Plate II, figs. 1 & 2) is a tall tree, with longer but flatter petiole glands than the other variety, *A. colubrina* var. *colubrina.* The pinna pairs of var. *Cebil* may be more numerous but the pinnae shorter than in the other variety. The leaflets of var. *Cebil* tend to be fewer, shorter, dilated in the middle, with prominent secondary veins. The heads may be larger and usually are borne axillary to the leaves and in a subterminal position, not frequently becoming arranged in racemose patterns in the branch apices. The legume is shorter, wider and thicker margined. The seeds are fewer and larger. This variety is the more variable of the two and is found in Argentina, Bolivia, Brazil, Paraguay and Peru. Specimens examined show it to be also the more widespread variety. It is broadly overlapping geographically with the distribution of var. *colubrina.*

Anadenanthera colubrina var. **colubrina** (Plate II, figs. 3 & 4) is a shorter tree with leaflets which tend to be linear and nitidulous above, with only the mid-vein prominent. The

PLATE II. Fig. 1. *Anadenanthera colubrina* var. *Cebil*, from Paraguay *(E. Hassler 7459)*, showing the shiny pod. Note the tendency for the inflorescences to be borne in a racemose pattern. Fig. 2. *Anadenanthera colubrina* var. *Cebil* in which the inflorescences are borne in a more markedly terminal racemose pattern, from Argentina *(R. E. Fries! s. n.)*. Fig. 3. *Anadenanthera colubrina* var. *colubrina* in flower, probably from Brazil *(Glaziou 5831)*. Here the tendency for inflorescences to be borne in terminal racemose-paniculate patterns is expressed fully. Fig. 4. *Anadenanthera colubrina* var. *colubrina* in fruit, from Brazil *(Widgren 2844)*, showing the long and uniformly contracted pods.

heads are distinctive in being always whitish in the bud, with the involucre, unlike that of the other variety, clearly visible below each head at that time. The heads are borne in paniculate patterns in the branch apices and have fewer flowers. The legume characteristically is elongated, and regularly contracted, often darker than in the other variety. *Anadenanthera colubrina* var. *colubrina* is the most easily recognizable element in the genus *Anadenanthera*, because of the distinctive arrangement of inflorescence. It is found in Argentina and Brazil. Specimens examined show this variety to have a more or less east coastal distribution and its representatives to be separated, at least locally, from those of var. *Cebil.*

Although previous authors have recognized infraspecific entities among the species here included in *Anadenanthera*, the names used in the present treatment appear nowhere to have been validated. In 1900, Malme suggested that *Piptadenia falcata* should not be distinguished from *P. peregrina.* Four years later, Chodat & Hassler referred *P. falcata* to varietal rank under *P. peregrina* but included neither a description nor reasons for the change. Similarly, Macbride suggested in 1943 that *P. macrocarpa* was very closely related to *P. colubrina* and that perhaps the former should be broadened to include the latter as a more southern-ranging variety.

MORPHOLOGY: **Habit.** — The representatives of *Anadenanthera* are feathery-foliaged, elegant-looking trees and shrubs. *Anadenanthera peregrina* var. *peregrina* ranges from a shrub to a tall tree, 3-27 m. high, with a trunk that usually is leaning and twisted. The contorted, irregular branches spread out above the middle of the trunk into an umbrella-like crown. Sometimes the trunk is divided at the base into several shafts. *Anadenanthera peregrina* var. *falcata* is reported to be small, a shrub or tree 4-8 m. high, shorter and thicker in aspect than the other individuals of the species. *Anadenanthera colubrina* var. *Cebil* ranges from a shrub to a tall tree, 3-30 m. high. It commonly is erect and without a divided trunk. *Anadenanthera colubrina* var. *colubrina* is a tree 3-24 m. high.

Plate III, fig. 1, shows a stand of *Anadenanthera peregrina* var. *peregrina* in northern Puerto Rico, in February, 1960.

PLATE III. Fig. 1. A stand of *Anadenanthera peregrina* var. *peregrina*, probably cultivated, in El Bosque Estatal de Cambalache, Puerto Rico. Fig. 2. Two trees of *Anadenanthera colubrina* var. *Cebil* cultivated in Orlando, Florida.

PLATE IV. Trunks of *Anadenanthera* spp. Fig. 1. *Anadenanthera peregrina* var. *peregrina* in El Bosque Estatal de Cambalache, Puerto Rico. Fig. 2. *Anadenanthera colubrina* var. *Cebil* in Orlando, Florida.

The slender trees were said to have been planted and were about 9-13 m. high.

Plate III, fig. 2, shows two somewhat storm- and cold-damaged trees of *Anadenanthera colubrina* var. *Cebil* in Orlando, Florida. They had been introduced as seedlings from São Paulo, Brazil, by Mr. and Mrs. Mulford B. Foster and had attained, by February, 1960, a height of about 13-15 m.

Trunk and branches. — The trunks may be unarmed or armed, especially toward the base, with mammillose projections. The bark is gray to black and becomes suberose in dry climates. In *Anadenanthera peregrina* var. *peregrina* the trunk has a diameter at breast height of 20-40 cm. When armed, the lower trunk produces conical to wedge-shaped projections, sometimes intensely when young. The bark is gray to nearly black with many small lenticels. *Anadenanthera peregrina* var. *falcata* reportedly produces bark often more than 5 cm. thick, and heavily suberose branches. *Anadenanthera colubrina* usually has a larger trunk than the above species, 30-50 cm. in diameter at breast height. The bark is grayish and smoother than in *A. peregrina*, even though it sometimes is striated with longitudinal fissures. The young twigs vary from very dark to light gray, with whitish or reddish warts. *Anadenanthera colubrina* var. *colubrina* has light gray bark, which is more or less smooth. When this tree is armed, the fortifications are short, fat and thorny.

Plate IV, fig. 1, shows the bark of *Anadenanthera peregrina* var. *peregrina*. In contrast, the relative smoothness of the bark of *A. colubrina* var. *Cebil* in Florida is shown in Plate IV, fig. 2. Orlando, Florida, lies at 28 degrees N. latitude, which is about the equivalent of Catamarca, Argentina, the source of the southernmost specimens of *A. colubrina* var. *Cebil* examined. This latitude may roughly represent the climatological limit in both hemispheres for *A. colubrina*.

Twigs and foliage. — These parts are more or less pubescent, or glaucous, rarely glabrous when young. They usually become glabrous with maturity. Individual specimens vary greatly. *Anadenanthera peregrina* var. *falcata* appears to be more densely puberulent when young, but more glabrous when mature, than var. *peregrina*. The twigs and foliage,

PLATE V. Fig. 1. *Anadenanthera peregrina* var. *peregrina* in El Bosque Estatal de Cambalache, Puerto Rico. Note the Bromeliad on the left trunk. Fig. 2. *Anadenanthera colubrina* var. *Cebil* in Orlando, Florida. Storm damage caused defoliation.

at least when dried, are also somewhat darker in var. *falcata*. *Anadenanthera colubrina* exhibits a higher degree of variation than does *A. peregrina*. While some specimens of *A. colubrina* var. *Cebil* are golden-red tomentulose (from Pernambuco) or partly puberulent, others are almost entirely glabrous. Specimens of var. *Cebil* appear, on the whole, to be less glabrous than specimens of var. *colubrina*.

Plate V, fig. 1, is a photograph looking up into the crowns of *Anadenanthera peregrina* var. *peregrina*. A view of the branches and leaves of *A. colubrina* var. *Cebil* is shown in Plate V, fig. 2.

Stipules. — These organs, which are only a few millimeters long, bristly and fugacious, are seen almost never on dried specimens. However, broad basal bracts in the leaf axils and enclosing the young inflorescence buds may persist.

Leaf. — The main and secondary axes of the bipinnately compound leaves (including the petioles) are often reddish when young. These parts are furrowed by a single longitudinal channel on the ventral surface. Dorsally, they are perfectly rounded and somewhat lighter in color and less puberulent than on the ventral side. The petioles are enlarged basally and are frequently a slightly different and darker color in the lower region. In *Anadenanthera peregrina* the leaf is 12-30 cm. long, and the petiole is darkened at the base. In *A. colubrina* the leaves tend to be shorter than they are in *A. peregrina*. They are 4-20 cm. long (petioles included in measurements of both species). The petiole base in this species is wrinkled transversely and may be greenish. *Anadenanthera colubrina* var. *colubrina* has a very deeply channeled rachis.

The pinna pairs vary in *Anadenanthera* from 7-35 or more per leaf, and each pinna may be 1.2-7 cm. long. The pinna pairs are opposite to subopposite, and the pinnae may extend, in *A. colubrina*, in a fine point 1.5-2 mm. beyond the ultimate pair of leaflets. In *A. peregrina* var. *peregrina* the pinna pairs are 10-30 or more per leaf, and each pinna is 2-5 cm. long. *Anadenanthera peregrina* var. *falcata* may be recognized by its fewer, 10-18, pinna pairs per leaf. *Anadenanthera colubrina* var. *Cebil* has 7-35 or more pinna pairs per leaf, each pinna being 1.2-7 cm. long. *Anadenanthera colubrina* var. *colubrina* bears 10-25 pinna pairs per leaf, and

PLATE VI. Terminal foliage of a representative of *Anadenanthera peregrina* var. *peregrina* in El Bosque Estatal de Cambalache, Puerto Rico.

each pinna is 3.5-7 cm. long, often with those toward the apex becoming shorter. These differences are relative and variable. For instance, a single specimen of *A. colubrina* var. *Cebil* was seen to exhibit a range of from 7 pinna pairs per leaf to 35 pinna pairs per leaf!

Plate VI shows terminal clusters of the leaves of *Anadenanthera peregrina* var. *peregrina*. The foliage is extended palmately at the tips of otherwise bare branches.

Glands. — These sessile protuberances appear to be elevations of portions of the margins bordering the channel that furrows the petiole and the rest of the main leaf rachis. In dried specimens they may be dark brown or black, rufous or white. One is found commonly on the petiole and 1-7 similar, smaller ones between or just below each of the ultimate pinna pairs. They may be absent. In *Anadenanthera peregrina* the main gland is dark, flattish, oval or oblong, .5-5 mm. long and located 5-15 mm. above the petiole base. In *A. colubrina* var. *Cebil* it more often is lacking than in *A. peregrina* or *A. colubrina* var. *colubrina*. One specimen of var. *Cebil* examined had two glands on one petiole. The main gland in var. *Cebil* is 1-5 mm. long and is found anywhere between the base of the petiole and the first pinna pair; it is flattened and, in living material, reddish. The smaller glands are 1-3 (rarely 7). In var. *colubrina* the main gland is 1-3 mm. long and found just above the petiole base; it is erect, 1-1.7 mm. high, with a deep pore, and is blackish in dried specimens. The smaller glands are 1-2 (rarely 6). The foliage glands are most uniform as to color, number, position, presence and size in *A. peregrina* var. *peregrina* and *A. colubrina* var. *colubrina*. In *A. colubrina* var. *Cebil* they may be inconsistent upon single specimens.

Leaflets. — The leaflets of *Anadenanthera* are sessile, opposite to subopposite, entire, at the base oblique or truncate, with margins usually ciliate or ciliolate. A pinna may bear 20-80 pairs of leaflets, each .9-8 mm. long and .5-1.5 mm. wide. In *A. peregrina* the leaflets usually are imbricate and at the apex more or less acuminate. In *A. colubrina* they are less often imbricate and at the apex relatively obtuse. In *A. peregrina* var. *peregrina* the leaflets are 25-80 pairs, 2-8 mm. long, usually straight and membranaceous. Those of *A. peregrina* var. *falcata* characteristically are more numerous, starting at 40 pairs, and longer, starting at 4.5 mm.; they tend to be falcate, coriaceous and nitid, with greater dorsiventral contrast than in var. *peregrina*. *Anadenanthera colubrina* var. *Cebil* bears 20-80 pairs of leaflets, each .9-6 mm. long and often dilated in the middle. The leaflets of var. *colubrina* are fewer and more standardized in number, 40-60 pairs per pinna; they also are longer and of more uniform lengths, 3-6 mm. These leaflets usually are glabrous except for the lightly ciliolate margins ending in an often acute apex. They are nitidulous but less so than in *A. peregrina* var. *falcata*. The leaflets of *A. colubrina* var. *colubrina* tend to be dorsiventrally distinct, opaque, and coriaceous in texture. In general, the leaflets of *A. colubrina* are shorter than those of *A. peregrina* and are more oblong in appearance. *Anadenanthera peregrina* var. *peregrina* and *A. colubrina* var. *Cebil* commonly have thinner, more membranaceous leaflets than do the other varieties of the two species.

Dried specimens of *Anadenanthera colubrina* var. *Cebil* often are grayish; some are green. In *A. peregrina* var. *peregrina* the foliage of herbarium material is brown or

Plate VII. Cleared and stained leaflets of *Anadenanthera* spp. Fig. 1. *Anadenanthera peregrina* var. *peregrina*, showing slightly excentric mid-vein (*R. Schomburgk 852*, Rio Branco). Fig. 2. *Anadenanthera peregrina* var. *falcata*, showing excentric mid-vein and finely reticulated end-veins (*Sellow 196*, Brasilia). Fig. 3. *Anadenanthera colubrina* var. *Cebil*, showing prominent secondary veins (*Gardner 1584*, Brazil).

green. Dried specimens of *A. peregrina* var. *falcata* and *A. colubrina* var. *colubrina* are darker, shinier, thicker and more glabrous in the leaflets than are those of the other varieties of the species. Living material of *A. peregrina* var. *peregrina* and of *A. colubrina* var. *Cebil* is bright green, and the leaflets wilt in minutes after a twig is cut.

The species of *Anadenanthera* are partly deciduous. Trees of *A. peregrina* var. *peregrina* growing in Puerto Rico were in full leaf during the relatively dry spring of 1960. *Anadenanthera colubrina* var. *Cebil* has almost persistent foliage which may be absent only at the end of the winter season. The extremities dry out in winter if frost occurs (Clos, 1929; Hieronymus, 1882). According to Hoehne, Kuhlmann & Handro (1941), the leaves of var. *colubrina* are lost in winter.

A fungus, *Ravenelia Cebil* Spegazzini (1909), has been described as parasitic on the leaves of the taxon here called *Anadenanthera colubrina* var. *Cebil.*

Heringer (1954b) published a brief but concise notice on the difference between the elements here called *Anadenanthera peregrina* var. *peregrina* and *A. colubrina* var. *Cebil.* He recognized the critical morphological differences between them and produced sketches of the peduncular involucre, the anthers and the leaflets. He did not, however, comment on the differences in venation suggested by the drawings. Plates VII-IX confirm these indications and illustrate, in addition, the patterns manifested in those entities which Heringer recognized but did not designate and which are treated here as *A. peregrina* var. *falcata* and *A. colubrina* var. *colubrina.*

The venation pattern basic to the species of *Anadenanthera* is a single, distinct vein which runs in nearly a straight line from the base to the apex of the leaflet. In Plate VII, fig. 1, the mid-vein of *A. peregrina* var. *peregrina* appears to be surrounded by a bundle sheath and is slightly eccentric. Plate VII, fig. 2, shows a leaflet of *A. peregrina* var. *falcata*, in which the end-veins seem to be more finely reticulated than in the other variety. Plate VII, fig. 3, shows a leaflet of *A. colubrina* var. *Cebil*, in which the secondary veins are much more prominent than in the other species. The leaflets of var. *Cebil* are also more variable, not only in venation but in size and shape, as well. In Plate VIII, fig. 1, are seen the marginal hairs which ordinarily are present on the leaflets but which usually do not survive processing. Some previously recognized varieties and forms lack distinctiveness and do not retain nomenclatural status in the present paper: Plate VIII, fig. 2, shows a leaflet of the type of *Piptadenia macrocarpa* var. *genuina* f. *puberula;* Plate VIII, fig. 3, shows a

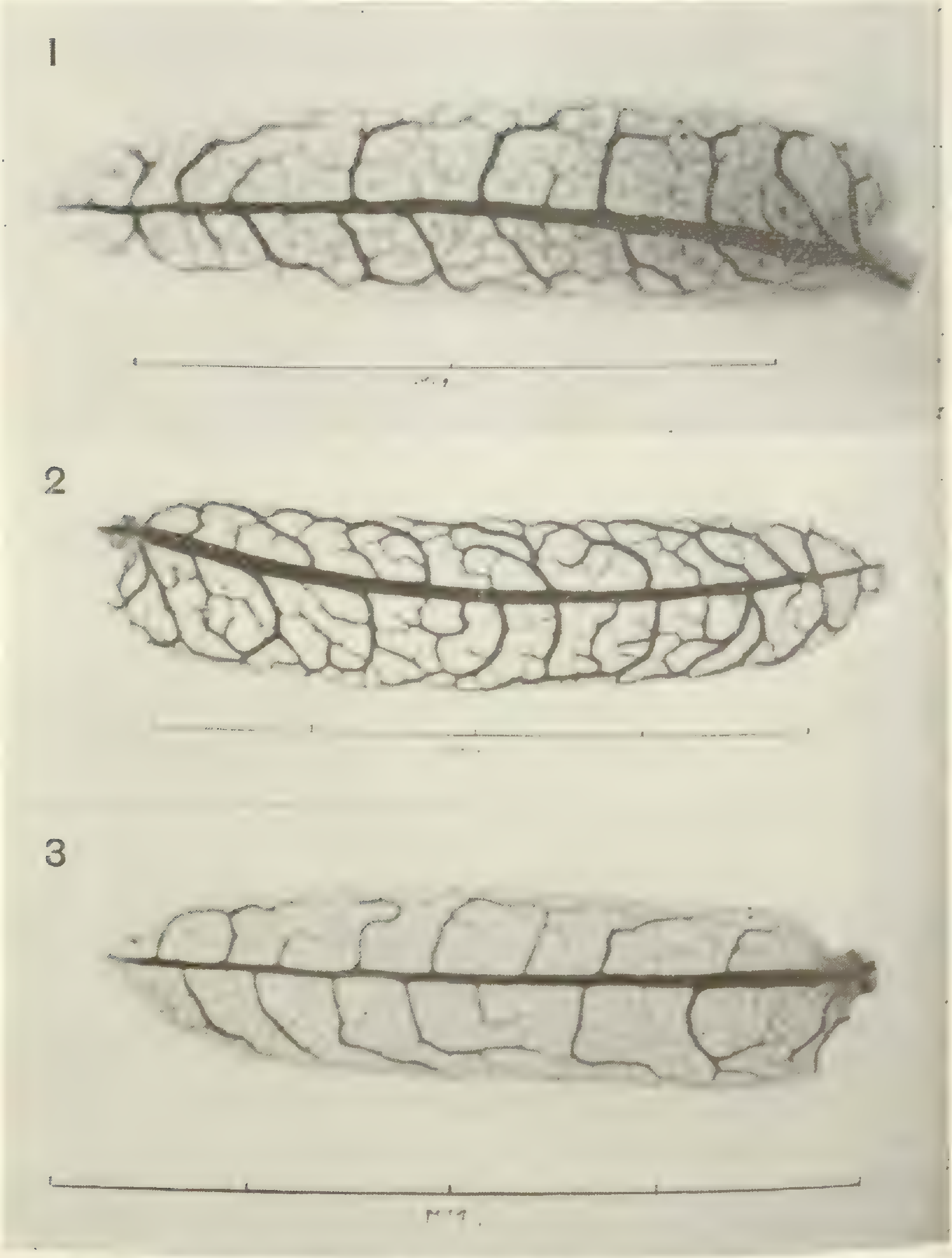


Plate VIII. Cleared and stained leaflets of *Anadenanthera colubrina* var. *Cebil.* Fig. 1. *Sellow 1412*, Brasilia. Note marginal hairs which usually do not survive processing. Fig. 2. *Hassler 7840*, Paraguay. Fig. 3. *Hassler 7466*, Paraguay.

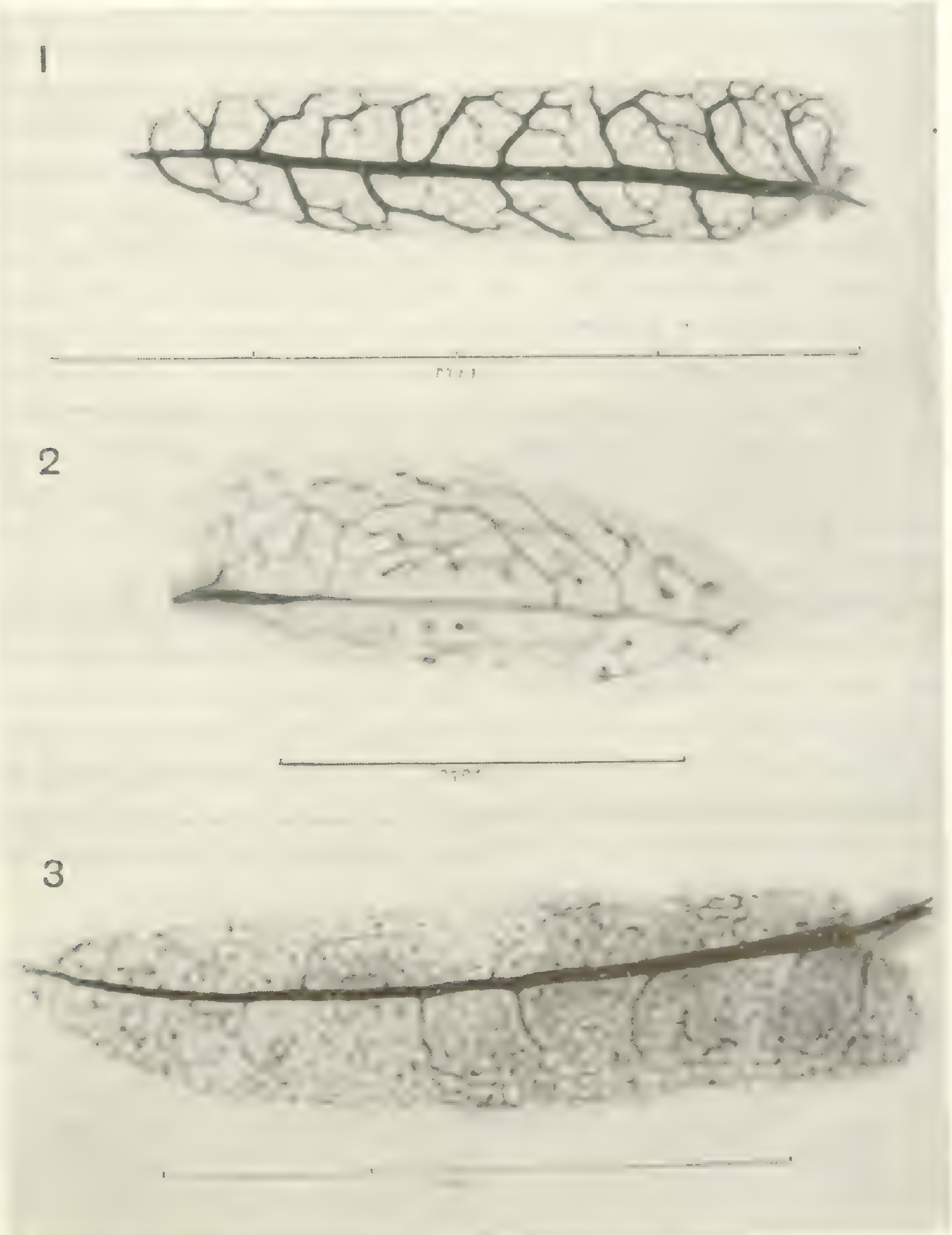


PLATE IX. Cleared and stained leaflets of *Anadenanthera* spp. Fig. 1. *Anadenanthera colubrina* var. *Cebil* (*Hassler* 8348, Paraguay). Fig. 2. *Anadenanthera colubrina* var. *Cebil* (*Hassler* 6688, Paraguay). Fig. 3. *Anadenanthera colubrina* var. *colubrina* (*Widgren s. n.*, Rio-Janeiro), showing less prominent secondary venation than in *A. colubrina* var. *Cebil.*

leaflet of the type of *P. macrocarpa* var. *Cebil* f. *microcarpa;* Plate IX, fig. 1, shows a leaflet of the type of *P. macrocarpa* var. *vestita.* The leaflet of the type of *P. Hassleriana* var. *fruticosa* in Plate IX, fig. 2, demonstrates one extreme form of vegetative variation common to the element here designated as *Anadenanthera colubrina* var. *Cebil.* In *A. colubrina* var. *colubrina,* Plate IX, fig. 3, the secondary veins are seen to be less prominent than in *A. colubrina* var. *Cebil.*

The value that can be placed on venation patterns for diagnostic purposes may not be consistent within the *Piptadenia* complex. Leaflets of the other genera included in Brenan's scheme in 1955 were not cleared for the present study, but observations with the dissecting microscope reveal the venation patterns to be somewhat variable even within the genera he cites. However, an adequate sampling was not available, and further studies on the problem are desirable.

Arrangement of inflorescences. — The inflorescences of *Anadenanthera* are heads. They are produced upon slender peduncles which are fasciculate, commonly in the axils of the compound leaves and subterminal. In *A. peregrina* the heads are almost always disposed as described and are 1-5 per fascicle. In *A. colubrina* var. *Cebil* the heads are 1-4 per fascicle and usually are disposed as above but also may be arranged in racemose patterns in the branch apices, with the subtending leaves more or less reduced. Such patterns are found in *A. peregrina* var. *peregrina* in rare instances. In *A. colubrina* var. *colubrina* the inflorescences are 2-4 (rarely 7) per fascicle and are arranged in paniculate patterns in the branch apices, with the subtending leaves usually absent. Occasionally, incompletely developed foliar organs are seen below the fascicles of the paniculately borne heads. Often, a few simple axillary and subterminal fascicles of heads are present also along the branches.

Peduncle. — *Anadenanthera peregrina* produces peduncles which are 1.75-4 cm. long and puberulous. In *A. peregrina* var. *peregrina* they are filiform. In *A. peregrina* var. *falcata* they are slightly thicker and may appear shorter than in the other variety because of the larger mature heads of var. *falcata.* Generally, in *Anadenanthera* the peduncles are 1-3 times as long as the heads. *Anadenanthera colubrina* produces peduncles 2-4 cm. long, either puberulous or glabrous, and a little thicker than filiform. In *A. colubrina* var. *colubrina* the peduncles become increasingly shorter toward the apex of the paniculate arrangement of the inflorescences. In both species of *Anadenanthera*, the peduncles thicken after fertilization.

Involucre. — Each peduncle bears around its upper portion two membranous bracts which are more or less united in an annular involucre about 1 mm. long. In *Anadenanthera peregrina* the involucre is puberulous, bidentate and campanulate. It is borne about three-quarters of the distance to the head and, in dried specimens, often is detached, encircling loosely the base of the peduncle and leaving a girdle-mark above. In *A. colubrina* the involucre may be glabrous or puberulous. It is borne just below the receptacle and does not become detached. The involucre of *A. colubrina* var. *Cebil* appears as a thin band or annulus which is not readily noticeable below the immature head. The growth of the flowers hides the involucre and may obstruct its further expansion. The involucre of *A. colubrina* var. *colubrina* is bidentate, like that of *A. peregrina*, but with the tips extended beyond a campanulate condition to nearly perpendicular to the main axis; it is borne just below the receptacle, as is characteristic for *A. colubrina*.

Inflorescence. — The small, sessile flowers of *Anadenanthera* are borne in globose-capitate heads, each with about 35-50 flowers crowded upon a globose-oblong receptacle commonly 5 mm. long. The mature heads usually are whitish or pale. The receptacle often is seen below the maturing 1-3 fruits as a pockmarked knob to which a few flowers may adhere. In *A. peregrina* var. *peregrina* the heads are greenish white to white, 10 or more mm. in diameter, including stamens, and several times shorter than the peduncles. In *A. peregrina* var. *falcata* the heads are white to creamy yellow and tend to be somewhat larger, up to 18 mm. in diameter. Upon one specimen of var. *falcata* auxiliary flower buds were found within the involucre of the peduncle. The heads of *A. colubrina* range in color from white to yellowish or, rarely, orangey. In var. *Cebil* they may be 15-20 mm. in diameter, including stamens. The heads of var. *colubrina* are only about 15 mm. in diameter; they reportedly are fragrant or aromatic and tend to have fewer flowers than do the heads in var. *Cebil* or *A. peregrina*. The heads of var. *colubrina* are minutely whitish-tomentose in the bud.

Bracteoles. — The individual flowers each are subtended by a linear-spathulate or deltoid bracteole commonly about half the length of the mature corolla and often equal in length to the variable calyx. The bracteole attains a maximum length of 2 mm. It is membranous-hyaline, delicately 1-veined, translucent and colorless to pale rufous in dried specimens, where the tip usually is darkened and lightly puberulent dorsally. The bracteole resembles in color, form, texture, venation and vesture the parts which make up the calyx and corolla. In the head it is much compressed and, in dried specimens, easily broken.

Calyx. — The small, sessile flowers of *Anadenanthera* have campanulate calyces which are 5-dentate and relatively variable in length for their size, being 0.5-3 mm. long. Differences in calyx length, as well as in color, have been seen within single heads and do not seem to be correlated with any other characters of the flowers. The calyx may be one-quarter to three-quarters the length of the corolla. It is, like the bracteole, membranous-hyaline, delicately 1-veined, translucent, and nearly colorless to pale rufous at the tips, which usually are at least lightly puberulent dorsally. Within a given element, vesture varies less in the flower parts than it does in the foliage. In some form, it is present nearly always in the inflorescence, even though limited to a few, fine epidermal hairs along the central vein at the tip of the bracteole, calyx lobe or petal. Specimens of *A. colubrina* which are otherwise glabrous still may retain this floral vesture.

Corolla. — The corolla consists of 5 free or lightly coherent petals. Like the calyx, its members are membranous-hyaline, delicately 1-veined, more or less translucent, and at least puberulent at the tips. The petals are off-white to flesh tone to pale rufous and sometimes, in dried specimens, dark at the tips. In *Anadenanthera peregrina* the corolla is 2-3.5 mm. long. In *A. colubrina* the corolla is 2.4-4 mm. long and often ruddier than in the other species. In *A. peregrina* the heads are more crowded and the flowers narrower than in *A. colubrina*. Usually the petals of both species cohere at a level more or less equal to the calyx tips. If the calyx is short, the petals may cohere to a point above the calyx tips; if the calyx is longer, the petals may cohere to a point below the calyx tips.

Androecium. — The stamens of *Anadenanthera* are 10 in number, 5-8 mm. long, glabrous and exserted, usually 2-3 times the corolla length. The filaments are free and filiform. The anthers are bilocular, elliptical and longitudinally dehiscent. In some specimens examined, the pollen appeared to have been released while the flowers were still in the bud. The pollen grains have nondescript, non-porous surfaces and are arranged in polyads, as Erdtman (1952) has indicated for many of the *Mimosoideae*, including some species of *Piptadenia*. According to Spegazzini (1923), in both *Piptadenia* (no species named) and *Anadenanthera*, the polyads are 12-grained, rarely 8-16, moderate-sized and semi-lenticular; they are paired in globose masses which are found 2-4 in each locule of the anthers. In *Piptadenia* (no species named), the individual grains are arranged in no particular order within the polyads; but in *Anadenanthera* four are central and eight peripheral (Spegazzini, 1923).

In *Anadenanthera peregrina* the anthers are eglandular in the bud; in *A. colubrina* they are glandular. The gland usually is stipitate-substipitate but may be sessile at one extreme or long-stipitate at the other. Glands may vary from sessile to stipitate upon a single individual. Each globose gland is attached at the extremity of the anther to the connective between the two chambers. Dried specimens suggest that the gland is soon caducous and frequently a brighter or darker shade of the anther color. Sometimes the gland is white. The anther commonly is paler than the filament. The overall color of the mature heads reflects that of the stamens, which darken with preservation and usually are off-white to golden red.

Gynoecium. — The simple ovary is unilocular, sessile-subsessile, many-ovuled and glabrous. It usually ranges from flesh color to dark in dried specimens and narrows into an elongated style, which enlarges apically into a tubular stigma at the level of or slightly above the anthers. (Because the filaments curl, the stamens appear shorter than they actually are). In *Anadenanthera peregrina* the fertilized ovary occasionally is reddish. In *A. colubrina* it may be similar or brighter red. The very young fruits are soon gray, at least in herbarium specimens; and the base begins to lengthen into a stipe.

Fruit. — The legume of *Anadenanthera* is more or less flattened, with a glabrous surface; it is unilocular, though often falsely septate. The legume is light to dark brown or reddish within and not pulpy. It dehisces along one suture only. Usually just one fruit ripens per head, rarely 2-3.

In *Anadenanthera peregrina* the fruit is oblongish to elongated, regularly, irregularly, vaguely, or not at all contracted between the seeds. The margins are slightly thickened, and the base is attenuate to obtuse. The surface is scurfy to verrucose, and dull; it is dark brown with rufous scales in dried specimens. In *A. peregrina* var. *peregrina* the legume is 5-35 cm. long (including the stipe but not the peduncle) and 1-3 cm. wide. It is more or less straight, with the apex mucronate to acuminate or, if the tip has broken off, rounded. In *A. peregrina* var. *falcata* the legume tends to be shorter than in the variety above, up to 22 cm. long, and with a narrower range of widths, 1.4-2.2 cm. It usually is falcate, with the apex mucronate or, if the tip has broken off, rounded. The margins of the pod of *A. peregrina* var. *falcata* may be also somewhat thinner than in the other variety. Falcate pods have been seen in dried material of *A. peregrina* var. *peregrina* from Venezuela, and specimens of var. *falcata* sometimes have straight pods.

In *Anadenanthera colubrina* the fruit is attenuate to obtuse or truncate at the base, and the apex mucronate to acuminate to cuspidate or, if the tip has broken off, rounded. The surface is smooth to reticulated, and nitid. In dried specimens the fruit is light, dark or reddish brown, or dark gray. In *A. colubrina* var. *Cebil* the legume is 10-32 cm. long (including the stipe but not the peduncle) and 1-3 cm. wide, straight to sometimes falcate, more or less oblongish to elongated. It is sinuate, or irregularly contracted, sometimes regularly contracted. The margins tend to be strongly thickened but occasionally are not at all so. Immature living material is bright yellow-green. The fruit of *A. colubrina* var. *Cebil* often is more oblong in dimensions, as well as thicker, than that of *A. peregrina*. In *A. colubrina* var. *colu-*

PLATE X. *Anadenanthera peregrina* var. *peregrina* in El Bosque Estatal de Cambalache, Puerto Rico. Fig. 1. Maturing fruit. Fig. 2. Seedling, showing enlarged root.

brina the legume is more distinctive, less variable, than in var. *Cebil.* It tends to be longer, starting at 15 cm., and narrower, up to 1.9 cm. Also the fruit in var. *colubrina* is striaght, very elongated, very regularly contracted, very flattened and thin, with margins thickened but narrower than in var. *Cebil.* At the base it is truncate, at the apex mucronate. The surface is finely reticulated, nitid and dark brown to dark gray in dried specimens.

Plate X, fig. 1, shows the nearly mature fruit of *Anadenanthera peregrina* var. *peregrina* in Puerto Rico, in early February. The legume is borne somewhat below the terminal leaves.

Seeds. — The seeds of *Anadenanthera* are 8-16, flat, and orbicular in outline. These smooth seeds are best described as wingless, but each has a rim or sharp margin. The seed is attached to a non-persistent, filiform funicle and is exalbuminous. The embryo is erect, the plumule conspicuously developed and divided. The thin cotyledons overlap and encase the stalk.

In *Anadenanthera peregrina* the seeds are very thin, orbicular to suborbicular in outline and a dark chestnut brown to black. They are shining and 10-20 mm. in diameter. The seeds of var. *peregrina* will germinate about 6 days after planting (Heringer, 1947).

In *Anadenanthera colubrina* the seeds are thin and dark chestnut brown. They are very shiny. The seeds of var. *Cebil* may attain oblong dimensions and are about 12-20 mm. in diameter, slightly larger than in *A. peregrina.* Mulford B. Foster has indicated in conversation that the seeds of var. *Cebil* germinate within only 2-3 days of planting. The seeds of *A. colubrina* var. *colubrina* are 10-16, more numerous than in the other taxa of *Anadenanthera.* They are orbicular to suborbicular, in contrast to the sometimes oblong seeds of var. *Cebil.* The seeds of var. *colubrina* are 12-15 mm. in diameter, uniformly smaller in size than is common in the seeds of var. *Cebil.*

WOOD ANATOMY: In 1954 (a, b) Heringer indicated that in *A. peregrina* var. *peregrina* the wood becomes reddish upon exposure to sunlight, the sapwood is little differentiated from the heartwood, and the annual growth rings are only slightly apparent. In *A. colubrina* var. *Cebil* the wood was said to be reddish, the sapwood much differentiated from the heartwood, the annual growth rings clearly apparent. Heringer described the element here considered as *A. colubrina* var. *colubrina*, unlike *A. colubrina* var. *Cebil*, as having the heartwood and sapwood not distinct one from another and the annual growth rings not very apparent.

In 1958, Brazier described the wood of *Anadenanthera*, in general, as being hard, heavy timber of fine texture, usually with an interlocked grain. The heartwood was said to weigh about 60 lbs. per cubic foot, and up to 70 lbs. in *A. colubrina* var. *Cebil*. *Anadenanthera colubrina* var. *colubrina* is distinguishable, in addition, by its fewer and larger vessels. (Neither Brazier nor Heringer mentioned the taxon here called *A. peregrina* var. *falcata*).

The differences between *Anadenanthera colubrina* var. *Cebil* and var. *colubrina* seem less extreme when the amount of anatomical variation reported for var. *Cebil* is considered. The literature on the wood of var. *Cebil* is relatively abundant, because that variety is important economically as a source of timber, particularly in Argentina. It not only has received many common names but has been divided, in colloquial usage, into several 'kinds' of trees. The descriptions of these trees are confusing. Discrepancies in reporting are found as to: presence or absence and color of the dark stripes (perhaps annual growth rings observed in tangential or radial section) in the wood; the thickness of the secondary walls of the fibers; the predominance of pore multiples or of solitary pores; the correlation of any of these tendencies one with another or with grosser characters such as extent of fortification at the base of the trunk, the color of the bark, the amount of splitting or warping likely to occur when the wood is cut and used commercially (Brazier, 1958; Cozzo, 1951; Herrera, 1921; Koehler, 1928; Lillo, 1917; Tortorelli, 1948).

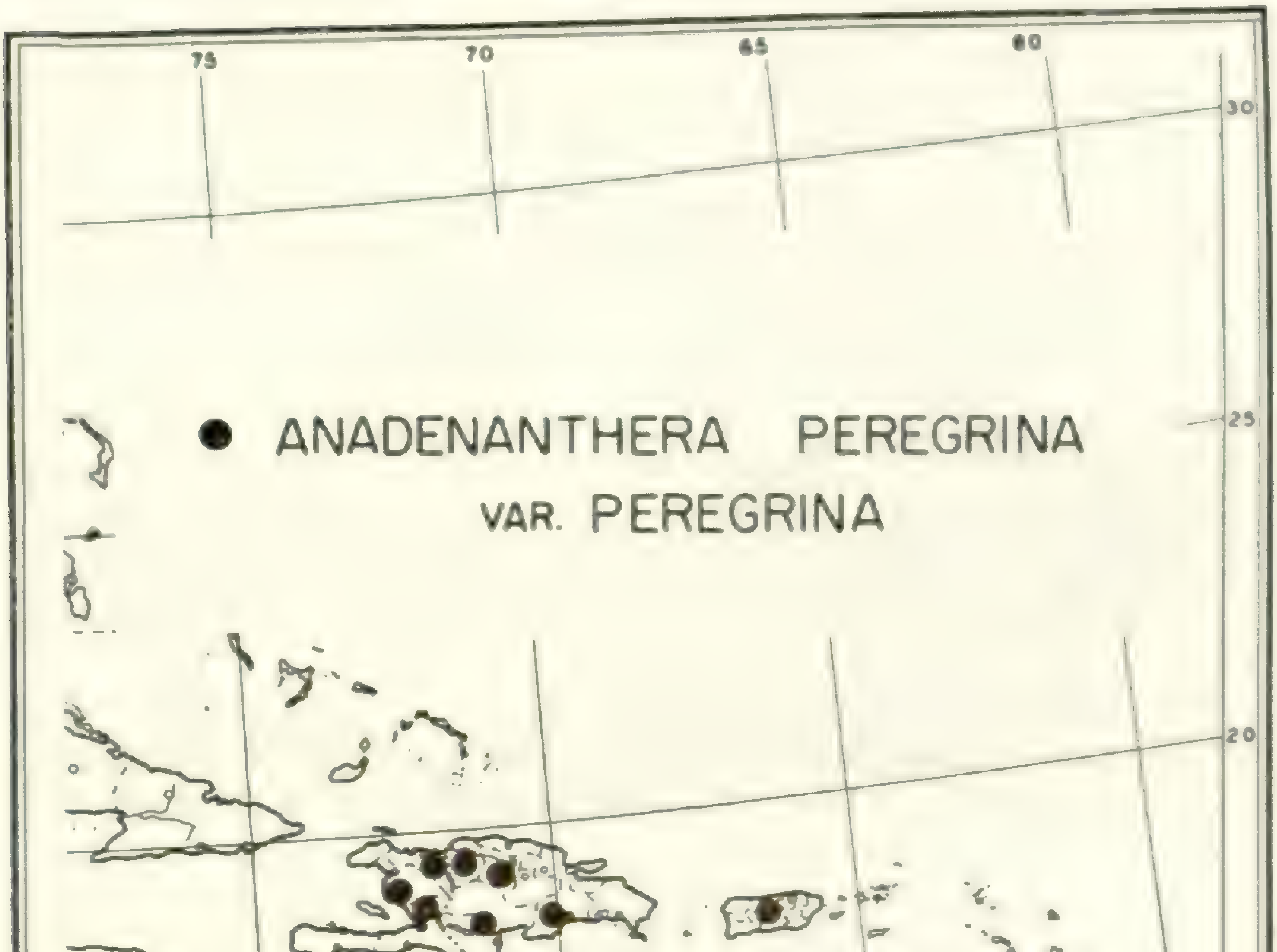
On the basis of field work and anatomical studies, Cozzo (1951) has concluded that, unusual as such variation may be below the generic level, it must be regarded as an expression of the natural variability of *A. colubrina* var. *Cebil*. In the light of available data, this may be the only reasonable conclusion. Since no patterns of variation correlatable with particular geographical areas or localities have been discerned, the characters involved in the variation exhibited in this taxon cannot be used to distinguish any further varieties as that category is employed here.

In summary, *Anadenanthera peregrina* has been studied but little anatomically. It is presumed to be fairly uniform in its wood characters. *Anadenanthera colubrina,* especially *A. colubrina* var. *Cebil,* appears to be variable in this respect as it is in others.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGICAL PREFERENCES: Representatives of the genus *Anadenanthera* are distributed widely throughout the tropical and subtropical New World. Maps 1 & 2 indicate partial distributions of the species examined in the course of this study.

Notes accompanying herbarium materials suggest ecological preferences of the species of *Anadenanthera.* In general, they may be described as occupants of savannas, as defined by Beard (1953). Although the species appear to be rather specific in requirements for drainage and light, they seem to be relatively adaptable with regard to altitude. *Anadenanthera peregrina* grows from sea level up to at least 1200 m. in altitude. *Anadenanthera colubrina* will survive up to 2100 m., possibly higher.

Anadenanthera peregrina has the greater north-south distributional range but may be slightly more selective of habitat than is the other species. On the island of Hispaniola, var. *peregrina* (Map 1) inhabits riversides, waste ground, plains, slopes, open ridges, chalky limestone, sandstone hills, roadsides and eruptive foothills, up to an altitude of 400 m. In Puerto Rico, it occurs in mountainous woods, along rivers, in riverside savannas, along roadsides, on hillsides and on red clay slopes. Venezuelan trees (Map 2) are reported variously as being forest dominants, belonging to secondary forests, inhabiting savannas, light forests and riversides, up to 750 m. alt. In British Guiana, *A. peregrina* var. *peregrina* is found in savannas and riverside forests. Brazilian representatives of *A. peregrina* are mostly from the *campos* (the Brazilian equivalent for the term savanna, according to Ducke & Black, 1953); they also are found along rivers in Pará. The South American collections examined of *A. peregrina* came from Colombia, Venezuela, British Guiana



MAP 1. Distribution of *Anadenanthera peregrina* var. *peregrina* in the West Indies, based on flowering specimens. Each symbol represents at least one collection. Only on Hispaniola are individual localities indicated.

MAP 2. Distributions of the species of *Anadenanthera* in South America, based on flowering specimens. Each symbol represents at least one collection. Where an element was represented only once for a state or country and without a specific locality, its symbol was placed in the center of that state or country.

and Brazil (Amazonas, Goyaz and Pará). The regions which these countries encompass are interspersed with savannas. North of the Orinoco River, savannas are found which occur on soils of Quaternary alluvia, a type of land which also is found in lowland Guiana. A broad belt of savanna country runs through Venezuelan Guiana; but, in most of British Guiana and the Amazon, savannas exist only as islands in the rain-forest (Beard, 1953).

Anadenanthera peregrina var. *falcata* (Map 2) is found in Minas Gerais, Brazil, in cut-over woods and on slopes. Specimens of this variety also have been collected in Mato Grosso, Paraná and São Paulo, Brazil, and in Paraguay. Areas of the same kind of land as is found supporting savannas in lowland Guiana and north of the Orinoco also are found in Paraguay (Beard, 1953).

Anadenanthera colubrina (Map 2) is limited in distribution to the southern hemisphere but appears to be adapted to more varied environments than is the other species. In Peru, *A. colubrina* var. *Cebil* occupies riversides, dry slopes and terraces, up to 2000 m. altitude. According to the literature, *A. colubrina* var. *Cebil* appears as a dominant tree in the xerophytic savanna-like formations of riparian valleys and on the western slopes, as far north as the Marañon Valley, at altitudes of 800-2700 m. (Weberbauer, 1945; Williams, 1945). Specimens were examined from Bolivia, where, according to Beard (1953), soils are to be found similar to those supporting savannas in Paraguay and lowland Guiana. Herbarium specimens from Paraguay indicate that *A. colubrina* var. *Cebil* grows along lakes and rivers, in mountains and on high plateaus, in rock declivities, valleys, fields, on woody riversides, in border woods and in forests. Common habitats for *A. colubrina* var. *Cebil* in northern Argentina include riverbanks with rich soil, forests, skirthills, *campos*, and the interiors of riparian mountains, at altitudes up to 1250 m. Specimens were examined from Catamarca, Corrientes, Jujuy, Misiones, Salta and Tucumán, Argentina. Sources from the literature report this variety as occurring in Argentina at altitudes of 340-900 m. in savanna country on laterite or sandy clays, in areas of winter frost. *Anadenanthera colubrina* var. *Cebil* is characteristic for the Región del Cebil, or Zona Chaqueña Occidental, in northwestern Argentina in the foothills of the Andes. The vegetation in that area is determined by high humidity and a long period of summer rains (Correa, 1925; Parodi, 1945; Tortorelli, 1948). Brazilian specimens from Minas Gerais have been collected on fertile ground in *pedreiras* (quarries, stone pits) and in the *matta* (heavy thickets, woods); in São Paulo, *A. colubrina* var. *Cebil* has been found in river areas. Other Brazilian specimens are from Bahia, Ceará, Maranhão, Mato Grosso, Pernambuco, Piauhy and Rio de Janeiro. According to Löfgren (1896), *A. colubrina* var. *Cebil* occupies, in São Paulo, transition zones between *campo*, or savanna, and more arid areas. The distribution of this variety appears to follow, in general, the patterns of geographic elevation associated with the Brazilian and Peruvian highlands.

Anadenanthera colubrina var. *colubrina* (Map 2) is restricted in its distribution, it seems, to Bahia, Paraná, Rio de Janeiro and São Paulo, Brazil, and to Misiones, Argentina. It generally is reported to occur along river edges; but one collection *(Glaziou 10592)*, made in Rio de Janeiro, is from the *restinga*. The last term, as it appears on the label, must refer to the old maritime beaches of white sand and black humus which are covered with shrubs and trees, in southeastern Brazil. (The term *restinga*, as used here, is not to be confused with the *restinga* of the Brazilian Amazon; nor should it be confused with the Amazonian *caatinga*, which it resembles superficially but from which it differs importantly with regard to rainfall and flora, according to Ducke & Black, 1953). Specimens of var. *colubrina* have been collected only up to 700 m. Information accompanying herbarium specimens is brief, and the literature is sparse. Hence, our present understanding of var. *colubrina* from a distributional and ecological viewpoint is limited. Luetzelberg (1922-23) reported this taxon as a constituent of what he called the tall *caatinga*. (This is not to be confused with the Amazonian *caatinga* above of Ducke & Black). Luetzelberg further indicated var. *colubrina* as occurring: in the xerophytic *mattas* uniting with this *caatinga*; in riverside areas from the northern part of Piauhy to northern Bahia; and in the mountains of extreme northeast Brazil. Souza (1945), too, mentions its presence in the arboreal *caatingas* of Brazil. However, the specimens examined from the areas indicated by Luetzelberg and Souza nearly all are better included in *A. colubrina* var. *Cebil.*

PHYLOGENY AND HISTORY OF DISTRIBUTION: Fossil evidence is lacking for the *Piptadenia* complex. However, it may be possible, on the basis of available information, to construct a picture of the probable origin and development of the genus *Anadenanthera.*

This small, strictly New World genus may be a relatively young offshoot of the *Piptadenia* complex. Such a probability is supported primarily by the arrangement of the flowers in a head, a character which could be explained as a reduction in the length of the axis of the spike found in all other members of the complex. A second argument may be presented from Spegazzini's report (1923) that the pollen grains of *Anadenanthera*, unlike those of the other members of the *Piptadenia* complex, are arranged in a particular order within the polyads.

If *Anadenanthera* did not arise as an offshoot of one of the existing genera of the *Piptadenia* complex, it may have originated from a more primitive stock ancestral, perhaps, to other genera as well, in that complex. Such an hypothetical stock could be thought of as having had the following characters: a spicate inflorescence, pollen grains un-ordered in the polyads, plus incompletely paratracheal parenchyma with high, multiseriate rays. The wood characters just mentioned are typical for *Anadenanthera* but are relatively primitive for the *Piptadenia* complex as a whole.

The evolutionary implications of the few distinguishing features of the two species of *Anadenanthera* are not readily understood. In morphological terms alone, the lack of anther glands in *A. peregrina* may be seen as a reduction, since those appendages are typical for members of the *Piptadenia* complex. On the other hand, the form and position of the involucre surrounding the peduncle appear to be more primitive in *Anadenanthera peregrina* than in *A. colubrina.* In var. *Cebil* of the last species the involucre apparently has been reduced from two partly fused, pointed bracts situated somewhat below the head to a thin band located just below the receptacle, as though the distance between the involucre and head had been telescoped, as well. The possible evolutionary significance of the different textures of the fruit of the two species is not easily recognized, as there is no obvious adaptation associated with either the scurfy-verrucose and dull condition in *A. peregrina* or the smooth-reticulated and shiny condition in *A. colubrina.* In some specimens of *A. peregrina* the pollen appears to have been released before the flowers opened, as stated earlier. If cleistogamy is suggested thereby as a mode of reproduction in this species, the likelihood for establishment of characters through random fixation also might be enhanced. The texture of the pod of *A. peregrina* may have been established by chance, rather than by direct selection; or it may be linked with another character or characters of survival value to the species. Since the pod textures are constant distinguishing characters for the two species of *Anadenanthera,* they must be as old as the species themselves and may be associated in their inception with much earlier times.

The geographical distributions of the two species of *Anadenanthera* suggest that the center of origin for the genus may be Brazil, where both species appear to be well represented today. This probability is enhanced by the fact that the preponderance of the American species of the *Piptadenia* complex grows in Brazil. Brazil may be a center for the evolution of New World Piptadenias in general.

If Brazil is the center of origin for the genus *Anadenantera, A. peregrina* is the species which has migrated the greater distance from that center. Within *A. peregrina,* var. *peregrina* is the more widespread and, by far, the more northern-ranging of the two component varieties. *Anadenanthera peregrina* var. *falcata* appears to be limited to the southern half of Brazil and perhaps exclusively represents *A. peregrina* in that region today.

The broad longitudinal distribution of *Anadenanthera colubrina* is predominantly that of var. *Cebil.* This variety radiates geographically outward in nearly all directions from the relatively limited area occupied by var. *colubrina.*

The areas occupied by *Anadenanthera peregrina* var. *falcata* and *A. colubrina* var. *colubrina* are sympatric and are presumed to lie within the postulated center of origin for the species of *Anadenanthera.* This center would fall in the Brazilian highlands, the southern part of which has been available for plant occupation since the Mesozoic and seems to have been the center of origin for other plant groups (Tryon, 1944). The altitudinal requirements and tolerances of the species of *Anadenanthera* today could reflect well such a history.

The present distributions of the species of *Anadenanthera* can be explained in terms which concur with the presumed geological history of the Amazon Valley as discussed by Seibert (1947) in a study of the genus *Hevea*. *Anadenanthera peregrina* var. *peregrina* may have achieved most of its present distribution at an early time, in association with the southern part of an ancient eastern mountain range whose flora extended into the Amazon Valley. This range appears to have extended from the Venezuela-Guiana land mass southward to connect with the ranges which today skirt the Amazon Valley in Goiás and Mato Grosso. The Amazon River is believed to have drained to the Pacific at that time. The relatively recent uplift of the Andes probably blocked that drainage, causing a huge inland lake to form in the central Amazon basin. Higher areas probably were isolated. *Anadenanthera peregrina* var. *peregrina* is represented today in the Amazon Valley within stands of savanna amid the rain-forest. These savannas are scattered from the edge of the Amazon flood plain both north and south toward the respective highlands of the Venezuela-Guiana land mass, and southeast Brazil. These savannas also are linked floristically with those two areas (Beard, 1953), and their flora is much older than that of the surrounding rain-forest (Ducke & Black, 1953). The representation of closely related taxa in both the Venezuela-Guiana land mass and in the highlands of southeast Brazil today is not limited to *Anadenanthera*. The primitive members of the euphorbiaceous genus *Micrandra* are found in the same two areas (Richard E. Schultes in conversation).

The characters by which *Anadenanthera peregrina* var. *falcata* is distinguished from var. *peregrina* may reflect climatic or ecological changes which could have occurred in southern Brazil subsequent to the northward distribution postulated for the original var. *peregrina*. The smaller habit, thickened vegetative parts and heavily suberose bark of representatives of var. *falcata* could be interpreted as drought adaptations. Whether this variety occurs, typically, in drier habitats than does var. *peregrina* is not known to me at this time.

Anadenanthera colubrina probably also arose in the Brazilian highlands. The movement of *Anadenanthera colubrina* var. *Cebil* westward into Paraguay, the mountains of Argentina, Bolivia and Peru most likely would have taken place subsequent to the northward migration of *A. peregrina* var. *peregrina* and after the establishment of the Orinoco or Amazon drainage of the Amazon basin lake. Prior to this drainage, it is believed, the lake drained southward through the Paraná-Paraguay Rivers system. Such a southern outlet could have prevented for some time the westward dispersion of *A. colubrina* var. *Cebil.*

Neither species of *Anadenanthera* is represented, to my knowledge, in western Amazonas nor in the Andes of northern Peru, Ecuador and Colombia. This circumstance is probably due to an inability of the representatives of *A. peregrina* var. *peregrina* to tolerate the true rain-forest conditions through which they would have to pass in a westward dispersal. There is equally little reason to believe that representatives of *A. colubrina* var. *Cebil* would descend from the Andes into lowland rain-forest. The absence of this taxon farther north in the Andes than north-central Peru may be due to the relative recentness of its dispersal. The greater variation exhibited by *A. colubrina* than by *A. peregrina* could be related to a more recent distribution for the first species, as well as, perhaps, to its being the younger species. The absence of specimens of either species from central Brazil may be due to lack of collections.

Anadenanthera colubrina var. *colubrina* appears to be limited in its distribution to an east coastal pattern. Its representatives are found within a relatively small geographic range, seem to have a maritime preference and apparently constitute the single entity from the *restinga. Anadenanthera colubrina* var. *colubrina* is characterized by the most highly evolved arrangement of inflorescences in the genus. The tendency for clusters of axillary, subterminal heads to become disposed in racemose-paniculate patterns in the branch apices is expressed fully only in this variety. A reported floral fragrance also is peculiar, within *Anadenanthera*, to var. *colubrina*. This fragrance and the relative showiness of the inflorescences, because of the manner in which they are borne, may be related to the unusually large size of the petiole glands. Mulford B. Foster indicated in conversation (1960) that the petiole glands, at least in *A.*

colubrina var. *Cebil*, nocturnally exude a substance attractive to insects and possibly related to pollination. Representatives of var. *colubrina* are specialized further in possessing fewer and larger vessels than are found in *A. colubrina* var. *Cebil*. *Anadenanthera colubrina* var. *colubrina* is also the most regular element in the genus with regard to measurable parts. These data suggest that var. *colubrina* probably arose from var. *Cebil* or an ancestral form of that variety. It may be that this variety has undergone relatively rapid evolution in some features coincident with certain ecological adaptations not wholly decipherable from either the specimens examined or the literature. Further study of *A. colubrina* var. *colubrina* should prove rewarding.

The species of *Anadenanthera* seem to have been adapted to savanna conditions and to various altitudes for an extended period. These trees, or shrubs, are semi-deciduous and apparently tolerant of long dry periods interspersed with only sporadic rains, which initiate the production of new foliage. The flat, rounded, light-weight seeds must be dispersed easily by floods, and even by winds. Their quick germination may be an adaptation to sudden inundations. Plate X, fig. 2, shows a subsoil enlargement of the basal portion of a young tree of *A. peregrina* var. *peregrina*, found in Puerto Rico. Such an enlargement could function in the storage of materials necessary for the tree during the period critical to establishment.

The species of *Anadenanthera* do not appear to hybridize in nature. Their flowering periods overlap, and their distributions are sympatric. Very little is known about the genetics of *Anadenanthera*. The chromosomes of *A. colubrina* var. *Cebil* are small and similar one to another. In this taxon the haploid number is 13, the commonest base number for the *Mimosoideae* (Atchison, 1951; Darlington & Wylie, 1956). The chromosome number of *Anadenanthera peregrina* var. *peregrina* still has not been determined (Berger, Witkus & McMahon, 1958).

The seeds of *Anadenanthera peregrina* are known as the sources of certain Indian preparations, particularly snuffs and beverages, for magical, medical, religious and stimulative purposes. The seeds of *A. colubrina* also seem to have been used for those purposes. However, it appears unlikely that man may have played an important role in effecting the present distribution of these species. The two species of *Anadenanthera* are similar in appearance, and chemical analyses of their fruits have shown them to be nearly identical with regard to the psychotomimetic compounds, bufotenine and its derivatives (M. S. Fish in a letter, January 7, 1958; Fish, Johnson & Horning, 1955; Pachter, Zacharias & Ribeiro, 1959; Stromberg, 1954). Therefore, *A. peregrina* and *A. colubrina* could have been used interchangeably where used at all. Furthermore, these species are distributed widely enough to be readily available to man throughout many parts of South America without cultivation. The fact that the genus consists of trees would discourage planting. The peoples who use *Anadenanthera* seeds in northern South America today are nomadic and seek the trees in savannas for seasonal harvesting.

The West Indies is the one region where man more reasonably accounts for the distribution of *Anadenanthera* than does distribution by natural means. There, *A. peregrina* var. *peregrina* is found today as a somewhat weedy tree, inhabiting roadsides and wastelands. Its representatives are remarkably uniform throughout the islands which suggests a relatively recent introduction. To the Island Arawak, who inhabited most of the islands where this taxon now is found, var. *peregrina* seems to have been of ritual importance. These Indians may have found it easier to plant the trees than to maintain communication with the mainland for their source of supply. The presence of war-like Carib on the smaller islands between them and South America would have added to the inconvenience. It is interesting to note that Safford (1916) believed that Linnaeus' original description of *A. peregrina* was based on a seedling grown in Europe from the New World. The seed most likely came from the West Indies or northern South America and may have been obtained through trade.

Anadenanthera peregrina var. *peregrina* is represented, among the specimens examined, from the islands of Hispaniola, Puerto Rico, Grenada, Tobago and Trinidad. Trinidad and Tobago are equitable floristically with the mainland (Beard, 1946). However, *A. peregrina* var. *peregrina* still may have been introduced into these islands. On a sheet of *Broadway 9258* from Trinidad it states that the species was planted and only "perhaps" a native tree. Beard (1946) did not include *A. peregrina* in a list of trees native to Trinidad. The only specimen of *A. peregrina* examined from the true Lesser Antilles, which have a distinctive flora, was from Grenada: *Beard 164*, labelled "In scrub on wasteland; apparently not native but naturalized." Collections simply could be lacking from the Lesser Antilles, but it seems more reasonable to suppose that *A. peregrina* is not found through most of these islands because the larger settlements of the Island Arawak existed predominantly in the Greater Antilles, with the exception of a sizeable community on Trinidad. For the most part, the Lesser Antilles were occupied by the Carib, for whom there are no indications of the use of *Anadenanthera* materials. In 1951, Cruxent presented surprising archaeological evidence suggesting that the Carib were relatively late-arriving, aggressive, colonizing groups from Central America. If this interpretation is correct, the absence of culture traits associated with *Anadenanthera* uses among the Carib can be explained by the fact that the genus is not represented and evidently was not known in Central America, or even in western Colombia. Finally, there would be no obvious reason why *A. peregrina* should not occur in Cuba if it were distributed naturally in the Greater Antilles, for the Cuban flora is predominantly South American in character (Seifriz, 1943). Rather, it is significant that the culture of the Island Arawak is not known to have extended westward beyond Hispaniola.

SYSTEMATIC TREATMENT

Anadenanthera Spegazzini, Physis 6: 313. 1923.

LECTOTYPE: *Anadenanthera peregrina* (L.) Speg.

Piptadenia Benth. Sect. *Niopa* Benth., Hook. Jour. Bot. 4: 340. 1841.
Lectotype: *P. peregrina* (L.) Benth.

Niopa (Benth.) Britton & Rose, Addisonia 12: 37. 1927.

Feathery-foliaged, often elegant-looking trees and shrubs of *South America* and the *West Indies*. Unarmed or the trunks armed toward the base with mammillose projections, the bark gray to black, becoming suberose in drier climates. Young twigs and foliage more or less pubescent, or glaucous, rarely glabrous, but becoming so with maturity. Stipules small, bristly and fugacious; but the broad basal bracts enclosing new shoots often persistent. Leaves alternate, bipinnately compound; main rachis and secondary rachises of young leaves often reddish and more or less channeled ventrally. Petioles usually enlarged basally and each commonly bearing, somewhere below the first pinna pair, a sessile, dark brown or black, rufous or white gland; 1-7 similar, smaller glands often borne along the main rachis, one between or just below each of the ultimate pinna pairs. Pinna pairs often many, 7-35 or more, each pinna 1.2-7 cm. long, opposite or subopposite. Leaflets sessile, opposite or subopposite, imbricate or expanded, not always borne to the very tip of the pinna, which may end in a fine point up to 2 mm. beyond the ultimate pair of leaflets. Leaflets many, 20-80 pairs per pinna, .9-8 mm. long, .5-1.5 mm. wide, entire, linear to dilated in the middle, oblong to lanceolate, straight to falcate, at the base oblique or truncate, at the apex acute to acuminate, apiculate or obtuse; margins usually ciliate or ciliolate; venation obscure, with one midvein and more or less prominent secondary reticulated veins; membranaceous to coriaceous and nitid or nitidulous, sometimes differing in texture and color dorsiventrally. *Inflorescence globose-capitate,* the heads 10-20 mm. in diameter, including stamens, greenish white to yellow or orangey, in fascicles of 1-7, minutely whitish-tomentose to glabrous in the bud; the heads axillary to the leaves and subterminal, or becoming arranged in racemose-paniculate patterns and terminal in the branch apices with the leaves reduced. Peduncles 1.75-4 cm. long, puberulous to glabrous, filiform or thicker, 1-3 times as long as the heads and each bearing a membranous, puberulous to glabrous annular involucre about 1 mm. long more than halfway up the axis or else directly under the receptacle and sometimes hidden by the mature head. *Flowers* about 35-50 per head, small, *sessile,* reportedly sometimes aromatic, crowded upon the globose-oblong receptacle about 5 mm. long and later visible as a pock-marked knob below 1-3 maturing legumes. Flowers each subtended by a linear-spathulate or deltoid bracteole half the length of the mature corolla. *Calyx* campanulate, .5-3 mm. long, *5-dentate,* about one-quarter to three-quarters the corolla length. *Corolla tubular-campanulate, 5-parted,* 2-4 mm. long; petals lightly coherent below the top of the calyx. Bracteoles, calyces and corollas membranous-hyaline, delicately 1-veined, translucent, and colorless to pale rufous at the tips in dried specimens, where often at least lightly puberulent dorsally. *Stamens 10,* 5-8 mm. long, glabrous, exserted, 2-3 times the corolla length, whitish to reddish in dried specimens; *filaments free,* filiform; anthers bilocular, elliptical and longitudinally dehiscent, each with or without a sessile to stipitate gland. *Ovary sessile-subsessile,* many-ovuled, glabrous, flesh color to darkish in dried specimens, narrowing into an elongated style which enlarges apically into a tubular stigma which may be at a level with or slightly above the anthers, because the filaments tend to curl and appear shorter than they are. *Legume* 5-35 cm. long (including the stipe but not the peduncle), 1-3 cm. wide, straight to falcate, oblongish to very elongated, more or less contracted, more or less flattened, sometimes thin, with margins slightly or strongly thickened; at the base attenuate to obtuse or truncate, at the apex mucronate to acuminate to cuspidate or, if the tip has broken off, rounded; surface glabrous, reportedly membranaceous to coriaceous but in dried specimens rigidly coriaceous and either smooth to reticulated, and nitid, or scurfy to verrucose, and dull; light brown, dark brown (sometimes with rufous scales), reddish brown or dark gray outside, light to dark brown or reddish within; *dehiscing along* *one suture only*, often falsely septate between the 8-16 thin, flat, orbicular to oblong, dark chestnut *brown to black*, shiny, *exalbuminous seeds* which are 10-20 mm. in diameter, wingless but *with a rim or sharp margin* and attached to a non-persistent, filiform funicle.

KEY

A. Anthers eglandular in the bud; involucre or scar ¾ of the way up the peduncle; legume scurfy to verrucose, and dull. .... (1. *A. peregrina*) B.

  B. Leaflets membranaceous, dull, straight; legume straight (northern Brazil, British Guiana, Colombia, Venezuela, West Indies). .... **1a. *A. peregrina* var. *peregrina*.**

  B. Leaflets coriaceous, nitid, falcate; legume falcate (southern Brazil, Paraguay). .... **1b. *A. peregrina* var. *falcata***

A. Anthers glandular in the bud; involucre just below the receptacle; legume smooth to reticulated, and nitid. .... (2. *A. colubrina*) C.

  C. Leaflets linear with the mid-vein more prominent than secondary venation; inflorescences borne in paniculate patterns in the branch apices; heads whitish in the bud; involucre with tips extended and noticeable below the immature head; legume very elongated, regularly contracted (Argentina, Brazil). .... **2a. *A. colubrina* var. *colubrina*.**

  C. Leaflets dilated in the middle, with prominent secondary venation; inflorescences fasciculate in the leaf axils and subterminal, or borne in racemose patterns in the branch apices; heads not whitish in the bud; involucre a narrow band not noticeable; legume relatively short and wide, often irregularly contracted (Argentina, Bolivia, Brazil, Paraguay, Peru). .... **2b. *A. colubrina* var. *Cebil*.**

1. Anadenanthera peregrina (L.) Speg.

Shrub to tall tree, 3-27 m. high. Trunk 20-40 cm. in diameter at breast height, usually leaning, twisted, sometimes divided at the base into several shafts; more frequently the contorted, irregular branches spread out above the middle of a solitary trunk into an umbrella-like crown. Bark gray to nearly black with many small lenticels; unarmed or lower trunk producing conical thorns or wedge-shaped projections, sometimes intensely so when young, becoming tubercular-verrucose, corky, rugose and, in drier climates, very thick. Young twigs and foliage puberulent, occasionally glaucescent; mature foliage glabrous or nearly so. Leaves, including petioles, 12-30 cm. long, the main rachis more or less channeled ventrally. Petioles somewhat darkened at their bases, 5-15 mm. above which each bears a flattish, oval or oblong gland .5-5 mm. long; 1-4 similar, smaller glands borne one between or just below each of the ultimate pinna pairs. Pinna pairs 10-30 or more, each pinna 2-5 cm. or more long, opposite or subopposite. Leaflets usually imbricate, 25-80 pairs, 2-8 mm. long, .5-1.5 mm. wide, linear, oblong or lanceolate, straight to falcate, at the base oblique or truncate, at the apex acute to acuminate to apiculate; venation obscure except for a single, nearly straight, slightly excentric mid-vein; membranaceous to coriaceous and nitid, sometimes differing in color and texture dorsiventrally. Heads 10-18 mm. in diameter, including stamens, greenish white to creamy yellow, in fascicles of 1-5, puberulous to glabrous in the bud; the heads axillary to the leaves and subterminal, rarely becoming arranged in racemose patterns in the branch apices. Peduncles 1.75-4 cm. long, puberulous, filiform or thicker, each bearing about three-quarters of the way up the axis a puberulous bi-dentate, campanulate involucre which becomes detached and slides down to encircle loosely the base of the peduncle. Calyx .5-2.6 mm. long. Corolla 2-3.5 mm. long. Stamens 5-8 mm. long; anthers eglandular in the bud. Legume 5-35 cm. long (including the stipe but not the peduncle), 1-3 cm. wide, straight to falcate, oblongish to elongated, regularly to irregularly, vaguely or not at all contracted between the seeds, more or less flattened, with margins slightly thickened; at the base attenuate to obtuse, at the apex mucronate to acuminate to cuspidate or, if the tip has broken off, rounded; surface scurfy to verrucose, and dull; dark brown with rufous scales in dried specimens. Seeds 8-16, very thin, flat, orbicular to suborbicular, dark chestnut brown to black, shiny, 10-20 mm. in diameter.

This species is found in the West Indies and South America, from 20 degrees N. latitude to 26 degrees S. latitude.

1a. **Anadenanthera peregrina** (L.) Speg. var. **peregrina**

Mimosa peregrina L., Sp. Pl. 520. 1753.
Acacia peregrina (L.) Willd., Sp. Pl. 4: 1073. 1806.
Piptadenia peregrina (L.) Benth., Hook. Jour. Bot. 4: 340. 1841.
Niopa peregrina (L.) Britton & Rose, Addisonia 12: 37. 1927.
Anadenanthera peregrina (L.) Speg., Physis 6: 313. 1923.
Acacia microphylla Willd., Sp. Pl. 4: 1073. 1806.
Inga Niopo Humb. & Bonpl. ex Willd., Sp. Pl. 4: 1027. 1806.
Mimosa Niopo (Humb. & Bonpl. ex Willd.) Poir., Dict. Encyc. Suppl. 1: 48. 1810.
Acacia Niopo (Humb. & Bonpl. ex. Willd.) Humb., Rélat. Hist. 2: 620-23. 1814-25.
Piptadenia Niopo (Humb. & Bonpl. ex Willd.) Spruce, Notes Bot. Amaz. 2: 426. 1908.
Mimosa parvifolia Poir., Dict. Encyc. Suppl. 1: 74. 1810.
Acacia angustiloba DC. Prod. 2: 470. 1825.
Mimosa? acacioides Benth., Hook. Jour. Bot. 2: 132. 1840.

TYPE: *Mimosa peregrina* L., a specimen from the Clifford Herbarium which is not locatable at present (W. T. Stearn in a letter, December 6, 1957). The type specimen was obtained from a seedling growing in the Clifford garden in Holland (Safford, 1916).

Mimosa peregrina, the earliest valid name by which *Anadenanthera peregrina* has been known, appeared in *Species Plantarum.* It was based on a fuller diagnosis in *Hortus Cliffortianus.* Although not complete, the diagnosis fits *A. peregrina* var. *peregrina* in all particulars except one, an incidental comparison to what now is known as *Mimosa cornigera* L. A photograph of the last species from the Linnaean Herbarium shows it to be represented by only a few bipinnately compound leaves subtended by large, thorny stipules. The description in *Hortus Cliffortianus* and *Species Plantarum* suggests that Linnaeus' familiarity with *M. cornigera* was founded exclusively upon that specimen. Considering this and the gross similarity of foliage characters among the *Mimosoideae*, Linnaeus' comment is more easily understood.

The type specimen of *Mimosa peregrina*, or the seed from which the plant supplying the type specimen was grown, most likely came from the West Indies or, possibly, northern South America. *Anadenanthera peregrina* var. *peregrina* is thought to have been introduced into the Antilles from the mainland. Linnaeus' description does not indicate why he applied the epithet *peregrina*. He may have been implying that the species was found from island to island or that it was not native to the West Indies.

It is apparent from photographs of *Acacia peregrina* (L.) Willd. obtained from Willdenow's herbarium (No. 19156) in Berlin that Willdenow interpreted Linnaeus' description as referring to the element here designated as the type-including variety of *Anadenanthera peregrina*. The flowers are not visible in detail, but the characteristic annular involucre can be seen loosely encircling the peduncle after having become detached. Willdenow's work is the earliest interpretation of Linnaeus' *Mimosa peregrina* as the element described here. Unless cogent evidence can be presented to the contrary, the traditional application of this name ought, I feel, to continue to be accepted.

SYNONYMY. *Acacia microphylla* Willdenow (1806) is included in the synonymy of *Anadenanthera peregrina* var. *peregrina* on the basis of the original description and a photograph of the type from the Willdenow Herbarium (No. 19155). Willdenow's only citation was "Habitat ad Caracas . . . Bredemeyer." Again, the flowers cannot be seen in detail, but the characteristic involucres are present. The specimen is *Bredemeyer s. n.*, from Caracas. Bredemeyer's South American and West Indian collections are from Venezuela, Curaçao and Puerto Rico, all areas where only the more northern-ranging *Anadenanthera peregrina* var. *peregrina* would occur.

The 1806 Willdenow edition of *Species Plantarum* contained the first scientific description of *Inga Niopo*. Willdenow attributed the name to Humboldt & Bonpland, and it evidently was based on material from the collection of those explorers, who had not yet published their famous account. Willdenow gave no collection number but mentioned the locality as being near Atures, which is along the Orinoco River. A photograph of the type from the Willdenow Herbarium (No. 19057) shows this plant, also, to belong to *Anadenanthera peregrina* var. *peregrina*. The specimen is fruiting and without flowers, so that it is not unreasonable for Willdenow to have thought it to be distinctive. Nevertheless, the foliage and fruits appear to be typical of var. *peregrina*, and the specimen comes from Atures. The epithet *Niopo* suggests that Humboldt & Bonpland were familiar with one of the native names attributed to var. *peregrina* in northern South America. It is referred to, in Willdenow, as having been used in place of tobacco. In 1810, Poiret placed *Inga Niopo* in the genus *Mimosa* but added nothing new in the way of interpretation. Four years later, in the first publication of *Personal Narrative . . .*, Humboldt mentioned, p. 405 (Vol. 2, 1900 ed.) ". . . the long pods of a mimosacea, which we have made known by the name of Acacia niopo, . . ." This was footnoted by the following: "It is an Acacia with very delicate leaves, and not an Inga". The author cited no material and must have been suggesting a correction of Willdenow's original publication. In 1824, the name appeared as *Acacia Niopo* (Humb.) H. B. & K., with an enlarged description but the flowers still unknown. Bentham (1841-42) subsequently placed this species in the synonymy of *Piptadenia peregrina*, doing so on the conviction that, although he had not seen Humboldt's material, its employment by the natives, as reported by Humboldt and by Schomburgk (in Bentham, 1840, p. 132), was adequate to identify it with *P. peregrina*. *Piptadenia Niopo* (Humboldt) Spruce was published in 1908. The author said that his specimens agreed so well in leaves, flowers and fruits with Kunth's description of Humboldt's *Acacia Niopo* that they undoubtedly belonged to the same species. But, as already stated, the flowers were unknown to Kunth and Humboldt and therefore not included in their diagnoses. Also, Spruce's description gives the anthers as glandular. An examination of one of the two numbers cited by Spruce, *1786* (BM), showed it to be a typical specimen of *Anadenanthera peregrina* var. *peregrina* in both flowers and fruits. This collection was made near the mouth of the Amazon River, at Santarém. Possibly, Spruce assumed that the anthers were glandular on the basis of Bentham's earliest formal description of *Piptadenia* (1841-42), which leads one to believe that all members of the genus have glandular anthers. Even Bentham's description of *P. peregrina* at that time did not indicate the eglandular condition of this species.

Mimosa parvifolia Poiret (1810) was based on *Acacia microphylla* Willdenow and represents a change of name plus a translation into French of the earlier author's Latin diagnosis.

The original description of *Acacia angustiloba* DeCandolle (1825) was not very extensive, but, nonetheless, it was stated that the anthers were eglandular and that the tree was from the Caribbean islands. DeCandolle suggested, with a question-mark, that *Acacia angustifolia* Lamarck might be a synonym of *A. angustiloba*. *Acacia angustifolia* does not belong to *Anadenanthera peregrina*, as is shown later in this paper. The type specimen of *Acacia angustiloba* therefore must be the uncited material upon which DeCandolle's description was based. A photograph of the type specimen, labelled *Acacia angustiloba* DC, on loan from the Delessert Herbarium (F), provides the means for identifying this species as belonging to *Anadenanthera peregrina* var. *peregrina*. The peculiar, loose annular involucres surround the peduncles. Although the locality is not given, the common name on the label, *Bois de tendre a Caillou*, suggests that the collection may have been made on Hispaniola.

Mimosa? acacioides Bentham (1840) was published before Bentham had described the genus *Piptadenia* but after he had begun to doubt the correctness of the then extant classification of some of the Mimosas and Acacias. Bentham subsequently (1841-42) placed this species under *Piptadenia peregrina*. The specimens he cited in the original description of *Mimosa? acacioides* agree with *Anadenanthera peregrina* var. *peregrina*. The original material was *Robert Schomburgk 852, 866*. I have examined the last number (F, BM, L and photographs from A, S, NY), from woods, skirting savannas in British Guiana. *Robert Schomburgk 852* (K) belongs to *A. peregrina* var. *peregrina* and was collected along the Río Branco. A sheet examined from Paris had two labels, one of which was *R. Schomburgk 852, 856;* the other label did not indicate the collector and was merely numbered "33". The material did not belong to *Anadenanthera*. Apparently, the collections had gotten mixed.

Shrub to tree, up to 27 m. high. Trunk with bark less than 5 cm. thick; branches not heavily suberose. Pinna pairs up to 30 or more. Leaflets 25 or more pairs, 2 or more mm. long, usually straight, membranaceous. Heads 10 or more mm. in diameter, including stamens; greenish white to white. Peduncles filiform. Legumes up to 35 cm. long, up to 3 cm. wide, usually straight.

DISTRIBUTION. Herbarium specimens indicate that *Anadenanthera peregrina* var. *peregrina* occurs in Brazil (Amazonas, Goyaz, Pará), British Guiana, Colombia and Venezuela. It probably is naturalized as found in the West Indies (Grenada, Hispaniola, Puerto Rico, Tobago and Trinidad). It has been cultivated on the islands and is reported not to be rare. In Puerto Rico conditions brought about by man no doubt have reduced its frequency. A small stand of cultivated trees exists in the Bosque Estatal de Cambalache in sunny, light mesophytic forest on flattish terrain in an area of well drained sandy, calcareous soil along the central northern coast at nearly sea level. According to herbarium labels, the species is found in the Greater Antilles at altitudes of up to 900 m. and in a number of environments. These include plains, scrub or waste lands, savannas along rivers and brooks, woody hillsides, sandstone valleys, eruptive foothills, open ridges and mountain slopes, on rocky soils and red clay slopes. In South America it is reported to be cultivated sometimes and to occur naturally from 70-1200 m. altitude as an occasional to frequent tree. It is abundant in savanna margins, characteristic of the edge of the *selva de galería*, and at times is given as a forest dominant. It is also a well known element in the *campos*, on open ground or in cut-over woods or secondary, light forest, in dry savannas and along rivers. In general, *A. peregrina* var. *peregrina* prefers semi-arid habitats.

REPRESENTATIVE SPECIMENS. **Brazil. Amazonas:** *R. L. Fróes 23075* (U); *Krukoff 6046* (A, BM, F, MO, NY, S, U, US). **Goyaz:** *Glaziou 21034*

(C, S). **Pará:** *Capucho 413* (F); *Dahlgren & Sella 21* (F); *Ducke 9884, 16519* (BM), *20186* (U); *de Oliveira 1949* (NY). **British Guiana:** *A. C. Smith 3217* (A, F, MO, NY, S, U, US). **Venezuela:** *Aristeguieta 1612* (US); *Pittier 8380* (F, GH, US), *11755* (A, NY, US), *13954* (F, NY, US), *14280* (US); *L. Williams 9973* (F, US), *12651* (F, S, US).

WEST INDIES. **Grenada:** *Broadway 1750* (F, GH, NY). **Dominican Republic:** *Ekman 12624* (S, US), *14278* (NY, S, US); *Fuertes 1561* (A, F, GH, NY, U, US); *Valeur 423* (NY). **Haiti:** *Ekman 3494* (A, S, US); *Holdridge 1069* (MO, NY, US). **Tobago:** *Broadway 3809* (GH, L, US).

Anadenanthera peregrina var. *peregrina* may be distinguished from *A. peregrina* var. *falcata* by the following characters: it is a taller tree with trunks and branches less corky. The pinna pairs tend to be more numerous but the leaflets fewer, shorter and straighter than in the other variety. The leaflets and other vegetative parts are generally thinner than in *A. peregrina* var. *falcata*. The heads are greener and may be smaller. The legume tends to be longer with a wider range of widths than in the other variety; it is usually straight; the apex is variable. Specimens examined show this more widespread and more northern-ranging variety to be found today from 20 degrees N. latitude to about 15 degrees S. latitude.

1b. **Anadenanthera peregrina** (L.) Speg. var. **falcata** (Benth.) comb. nov.

Based on *Piptadenia falcata* Benth., Hook. Jour. Bot. **4**: 341. 1841.

Piptadenia peregrina (L.) var. *falcata* (Benth.) Chod. & Hass., Bull. Herb. Boiss. II. **4**: 561. 1904.

Anadenanthera falcata (Benth.) Speg., Physis **6**: 313. 1923.

HOLOTYPE: *Sellow 196*, Brasilia (K, with photographs of the type at A, NY). The material for the original description was cited by Bentham as "— Brazil, Sello." Of four sheets examined from Kew belonging to this variety and collected by Sellow, the one cited is the only one numbered.

Shrub to tree, up to 8 m. high. Trunk with bark more than 5 cm. thick; branches heavily suberose. Vegetative organs often densely puberulent when young. Pinna pairs up to 18. Leaflets 40 or more pairs, 4.5 or more mm. long, usually falcate, coriaceous, nitid on the dorsal surface. Heads up to 18 mm. in diameter, including stamens; white to creamy yellow. Peduncles thicker than filiform. Legume up to 22 cm. long, 1.4-2.2 cm. wide, usually falcate; at the apex mucronate or, if the tip has broken off, rounded.

DISTRIBUTION. Specimens come from Brazil (Matto Grosso, Minas Geraes, Paraná, São Paulo) and Paraguay. This variety is common in the *campo cerrado;* in rocky fields; on high plains, in valleys; and along rivers.

REPRESENTATIVE SPECIMENS. **Brazil. Minas Geraes:** *Regnell III 517* (C, S, US). São Paulo: *de Andrade 26646* (A, NY, US); *Regnell III 517 xa* (S), *III 717x* (S). **Paraguay:** *Hassler 4506, 5292* (A, BM, NY), *10516* (A, C, MO, NY, S, US), *10516a* (A, BM). Also representative, though lacking a number, is a sheet labelled "Herb. Reg. Berolinense. *Piptadenia falcata* Benth. Brasilia. Sellow legit." (K).

Anadenanthera peregrina var. *falcata* may be distinguished from *A. peregrina* var. *peregrina* by the following characters: it is a much shorter tree with suberose trunks and branches, thicker leaves and peduncles, resembling *Stryphnodendron* on herbarium sheets. Although often densely puberulent when young, the vegetative organs of var. *falcata* become more glabrous with maturity than do those of the other variety. The pinna pairs tend to be fewer but the leaflets more numerous, longer and more often falcate than in var. *peregrina*. The leaflets are generally coriaceous, contrast dorsiventrally and are darker in dried specimens than those of the other variety. The heads are yellowish and may be larger. The legume tends to be shorter with a narrower range of widths than in var. *peregrina*; it usually is falcate; the apex is mucronate or, if the tip has broken off, rounded. Specimens examined show this less widespread and more southern-ranging variety to be found today from about 15 degrees S. latitude to 25 degrees S. latitude.

2. **Anadenanthera colubrina** (Vell.) Brenan

Shrub to tall tree, 3-30 m. high. Trunk 30-50 cm. in diameter at breast height, commonly erect. Bark 2-5 cm. thick, grayish, smooth or rugose, sometimes striated with small longitudinal fissures; unarmed or with mammillose protuberances. Young twigs and foliage partly puberulent, sometimes tomentellose, usually becoming glabrous with maturity. Leaves, including petioles, 4-20 cm. long, the main rachis channeled ventrally. Petioles scatteredly pubescent, at their bases horizontally wrinkled and each commonly bearing, somewhere below the first pinna pair, a flattened or erect, oval to disciform, more or less centrally depressed gland 1-5 mm. long; 1-3 (rarely to 7) similar, smaller glands borne one between or just below each of the ultimate pinna pairs. Pinna pairs 7-35 or more, each pinna 1.2-7 cm. long, usually opposite. Leaflets not always borne to the tip of the pinna, which may end in a fine point 1.5-2 mm. beyond the ultimate pair of leaflets. Leaflets imbricate or expanded, 20-80 pairs, .9-6 mm. long, .5-1.5 mm. wide, linear or slightly dilated in the middle, oblong to lanceolate, usually straight (not falcate), and the base oblique or truncate, at the apex acute to apiculate or obtuse; venation obscure, or with a straight or nearly straight, slightly excentric mid-vein, and more or less prominent secondary reticulated veins; membranaceous to coriaceous and nitidulous above, sometimes differing in color and texture dorsiventrally. Heads 15-20 mm. in diameter, including stamens, white to whitish yellow to orangey, in fascicles of 1-7, minutely whitish-tomentose to nearly glabrous in the bud; the heads axillary to the leaves and subterminal, or becoming arranged in racemose-paniculate patterns in the branch apices with the leaves reduced or absent. Peduncles 2-4 cm.

long, puberulous to glabrous, thicker than filiform, each bearing just below the receptacle and often hidden by the mature head a narrow, more or less glabrous annular involucre. Calyx .6-3 mm. long. Corolla 2.5-4 mm. long. Stamens 5-8 mm. long; anthers each with a caducous gland. Legume 10-32 cm. long (including the stipe but not the thickened peduncle), 1-3 cm. wide, straight to sometimes falcate, oblongish to very elongated, regularly contracted to sinuate, or irregularly contracted where seeds have aborted, sometimes very flattened and thin, with margins often strongly thickened, even though sometimes narrow; at the base attenuate to obtuse or truncate, at the apex mucronate to acuminate to cuspidate or, if the tip has broken off, rounded; surface smooth to reticulated, and nitid; light, dark or reddish brown or dark gray in dried specimens. Seeds 8-16, thin, flat, orbicular to oblong, dark chestnut brown, very shiny, 12-20 mm. in diameter.

The species is found in South America, with an approximate distribution of 0-30 degrees S. latitude.

2a. **Anadenanthera colubrina** (Vell.) Brenan var. **colubrina**
Mimosa colubrina Vell., Fl. Flum. **11**: tab. XVI. 1790.
Acacia colubrina (Vell.) Mart., Herb. Fl. Bras. 107. 1837.
Piptadenia colubrina (Vell.) Benth., Hook. Jour. Bot. **4**: 341. 1841.
Anadenanthera colubrina (Vell.) Brenan, Kew Bull. **2**: 182. 1955.

TYPE: the plate of *Mimosa colubrina*, tab. XVI, in Velloso's *Flora Fluminensis* of 1790. This drawing delineates the fruits and foliage. It is not greatly detailed but conforms to the characters of *Anadenanthera colubrina* var. *colubrina*. The interpretation of the type is aided by Velloso's description, which was not published until 1881. The description refers to the plate and characterizes the plant as an unarmed *Mimosa* with bipinnately compound leaves, the leaflets many-paired and lanceolate-linear; the legume linear, torulose or undulate. The author further designated this element as a few-branched tree, with the outermost pinnae of decreasing length, the legume curved on both margins, reticulate and briefly pedicellate; the seed globose. The pod was said to be long and, according to the common coastal expression, 'colubrine'. The inflorescence was described as globose-capitate.

Shrub to tree, up to 24 m. high. Main leaf rachis deeply channeled ventrally. Petioles each bearing just above the base an erect, deep-pored, blackish gland up to 1.7 mm. high and up to 3 mm. long; 1-2 (rarely to 6) smaller glands borne between the ultimate pinna pairs. Pinna pairs up to 25, becoming shorter toward the leaf apex, each pinna 3.5 or more cm. long. Leaflets 40-60 pairs 3 or more mm. long, usually linear, nitidulous above. Venation with the mid-vein more prominent than secondary veins. Heads about 15 mm. in diameter, including stamens, in fascicles of 2-4 (rarely to 7), minutely whitish-tomentose in the bud with the annular involucre expanded and visible below each head at that time; the heads borne in paniculate patterns in the branch apices, with the peduncles becoming increasingly shorter toward the apex of the paniculate arrangement of the inflorescences. Legume 15 or more cm. long, up to 1.9 cm. wide, very elongated, regularly contracted, very flattened and thin, with margins thickened but narrow; at the base truncate, at the apex mucronate; surface finely reticulated, nitid; dark brown to dark gray in dried specimens. Seeds 10 or more, orbicular to suborbicular, up to 15 mm. in diameter.

DISTRIBUTION. Herbarium specimens were examined from Argentina (Misiones) and Brazil (Bahia, Paraná, Rio de Janeiro, São Paulo). The variety has been collected in woods, along rivers and in *restingas*. The material comes from localities of no greater altitude than 700 m.

REPRESENTATIVE SPECIMENS. **Brazil. Bahia:** *Ule 6955* (L). **Paraná:** *Dusén 11253* (S); *Tessmann 6021* (A, U). **Rio de Janeiro:** *Campos Porto 10415* (U), *10416* (S, U, US); *Glaziou 10592* (A, C), *10596* (C, NY, S); *Widgren s. n.* (S). **São Paulo:** *Hoehne 1030* (GH), *28582* (A, F, GH, NY, S). Other numbers from Brazil, but lacking locality designations, are *Pohl 1445* (F, NY), *s. n.* (US); *Widgren 419* (S).

Anadenanthera colubrina var. *colubrina* may be distinguished from *A. colubrina* var. *Cebil* by the following characters: it is a shorter tree. The main leaf rachis is more deeply channeled ventrally. The petiole gland tends to be shorter but erect. The pinna pairs may be fewer but the pinnae longer than in *A. colubrina* var. *Cebil*, with the pinnae becoming noticeably shorter toward the leaf apex. The leaflets tend to be fewer, longer and more often linear and nitidulous above, with only the mid-vein prominent. The heads may be smaller than in *A. colubrina* var. *Cebil* and always are whitish in the bud, with the two tips of the annular involucre extended and visible below each head at that time. The heads are borne in paniculate patterns in the branch apices, with the subtending leaves reduced to absent. The flowers are fewer per head than in *A. colubrina* var. *Cebil*, and reportedly are aromatic. The legume is longer and narrower than that of *A. colubrina* var. *Cebil*, very elongated, regularly contracted, flatter and thinner, with margins thickened but narrower than in the other variety; the base is usually truncate, the apex mucronate, with the surface finely reticulated, nitid, dark brown to dark gray in dried specimens. The seeds of *A. colubrina* var. *colubrina* are more numerous and smaller. This variety tends to be generally more uniform in appearance than *A. colubrina* var. *Cebil*. Specimens examined show this less widespread variety to be found today from about 12 degrees S. latitude to 27 degrees S. latitude, overlapping geographically with the distribution of *A. colubrina* var. *Cebil*.

2b. **Anadenanthera colubrina** (Vell.) Brenan var. **Cebil** (Griseb.)
comb. nov.

Based on *Acacia Cebil* Griseb., Goett. Abh. **19**: 136. 1874.
Piptadenia macrocarpa Benth., Hook. Jour. Bot. **4**: 341. 1841.

P. macrocarpa Benth. var. *genuina* Chod. & Hass., Bull. Herb. Boiss. II. 4: 559. 1904.
P. macrocarpa Benth. var. *genuina* Chod. & Hass. f. *puberula* Chod. & Hass., ibid.
P. macrocarpa Benth. var. *Cebil* (Griseb.) Chod. & Hass., Bull. Herb. Boiss. II. 4: 560. 1904.
P. macrocarpa Benth. var. *Cebil* (Griseb.) f. *rupestris* Chod. & Hass., ibid.
P. macrocarpa Benth. var. *Cebil* (Griseb.) f. *microcarpa* Chod. & Hass., ibid.
P. macrocarpa Benth. var. *vestita* Chod. & Hass., ibid.
P. macrocarpa Benth. var. *plurifoliata* Hoehne, Comm. Linh. Tel. Annex. 5 (Bot. Pt. 8) : 28. 1919.
Anadenanthera macrocarpa (Benth.) Brenan, Kew Bull. 2: 182. 1955.
Piptadenia microphylla Benth., Hook. Jour. Bot. 4: 341. 1841.
P. Cebil (Griseb.) Griseb., Goett. Abh. 24: 121. 1879.
P. Hassleriana Chod., Bull. Herb. Boiss. II. 4: 560. 1904.
P. Hassleriana Chod var. *fruticosa* Chod. & Hass., ibid

HOLOTYPE: *Lorentz 194.* Although no material was cited in the original publication of *Acacia Cebil* Grisebach, the description evidently was based on a collection of Lorentz. The description appeared not only in the journal referred to above, cited by *Index Kewensis*, but also earlier in the same year in *Plantae Lorentzianae.* I have examined *Lorentz 194* from Grisebach's herbarium. It is labelled *Acacia Cebil.*

The original description of *Acacia Cebil* lacks references to flowers and *Lorentz 194* has no flowers. However, both are consistent with the fruit and foliage characters of the present interpretation of *Anadenanthera colubrina* var. *Cebil.* In 1879, Grisebach transferred *Acacia Cebil* to the genus *Piptadenia.* He added a description of the flowers and stated that he doubted whether the species was satisfactorily distinguishable from *P. macrocarpa.* Grisebach treated *Piptadenia Cebil* as separate from *P. macrocarpa* because the petiole gland was absent and the legume contracted between the seeds of *P. Cebil.* In 1904, Chodat & Hassler published *P. macrocarpa* var. *Cebil*, based on Grisebach's name. They distinguished the variety on the basis of the glabrosity of the leaflets and the legume's being up to 20 cm. long by 2.2 cm. wide. They described *P. macrocarpa* var. *Cebil* as a tree 15-20 m. high, from Paraguay. All of the foregoing characters are includable in *Anadenanthera colubrina* var. *Cebil*, as here conceived. *Cebil* is the common name probably most often associated with this variety in northwestern Argentina, where abundant collections have been made.

SYNONYMY. *Piptadenia macrocarpa* Bentham (1841) is included in the synonymy of *Anadenanthera colubrina* var. *Cebil* on the basis of the original description and material examined. Bentham did not designate a holotype as such from the original material, which he cited as " — Brazil, Pohl, Sello; Gardner 1584. No. 1107 of Martius, Herb. Pl. Bras. in either this or the preceding species." The word "in" in the last sentence is a misprint for "is." The "preceding species" is *P. peregrina.* However, *Martius 1107* agrees with Bentham's *Piptadenia macrocarpa.* I have examined two sheets of that collection bearing flowers (BM, S). Nevertheless, Bentham's doubt about the identity of *Martius 1107* at the time of publication and his citing *Gardner 1584* ahead of it suggest that Gardner's number should have precedence in the interpretation of the type of *Piptadenia macrocarpa*. *Gardner 1584* also fits the description of *P. macrocarpa*. I have examined three sheets of that collection (BM, GH, NY). This leaves as the only other possibilities the unnumbered collections of Pohl and Sellow. Although they are the first named by Bentham, the exact sheets examined by Bentham may not be ascertained easily. *Gardner 1584* seems to be the reasonable choice in interpreting the type, as it is the first number cited in Bentham's description, fulfills the characters ascribed to *P. macrocarpa* and is flowering. *Gardner 1584*, *Martius 1107*, and the description of *P. macrocarpa* all agree well with *Anadenanthera colubrina* var. *Cebil*, as here conceived. The original description of *Piptadenia macrocarpa* gives the pods as very smooth. The flowers in the two collections examined have glandular anthers and heads which are axillary and subterminal. *Gardner 1584* was collected in Ceará, Brazil, which is outside of the known range of *Anadenanthera colubrina* var. *colubrina*.

In 1904, Chodat & Hassler published three varieties of *Piptadenia macrocarpa: genuina*, *Cebil* and *vestita*. Specimens bearing the label *P. macrocarpa* var. *genuina*, if correctly identified now should be called *Anadenanthera colubrina* var. *Cebil*. Under *Piptadenia macrocarpa* var. *genuina*, Chodat & Hassler published f. *puberula*, with puberulent leaflets and up to 23 pinna pairs per leaf. I have examined material of the type, *Hassler 7840*, from near Bellavista, Paraguay (BM, NY) and identified it as *Anadenanthera colubrina* var. *Cebil*.

Under *Piptadenia macrocarpa* var. *Cebil*, Chodat & Hassler distinguished two forms, of which I have examined the types. *Piptadenia macrocarpa* var. *Cebil* f. *rupestris* has 10-12 pinna pairs per leaf, the pairs up to 1 cm. apart, and the leaflets perfectly glabrous. The only unusual character is the relatively wide spacing between the pinna pairs. The type is *Hassler 6375*, from central Paraguay (BM, NY). *Piptadenia macrocarpa* var. *Cebil* f. *microcarpa* was described as producing a legume scarcely 10 cm. long and 1.8 cm. wide, as well as inflorescences arranged in subpaniculate patterns. The specimen did not seem to represent a special taxonomic entity. Despite the subpaniculate arrangement of the heads, it probably is better placed in the more variable *Anadenanthera colubrina* var. *Cebil* than in *A. colubrina* var. *colubrina*. It has a very short legume and was collected outside the range of var. *colubrina*. The material examined was *Hassler 7459* (A, BM, MO, NY, S) and *7466* (A, BM, C, MO, NY, S), both from near Concepción, Paraguay.

Piptadenia macrocarpa var. *vestita* of Chodat & Hassler has conspicuously puberulent foliage and heads which are arranged in racemose patterns. It falls within the wide range of variation found in *Anadenanthera colubrina* var. *Cebil:* and the type, which I have examined, was collected in a region where *A. colubrina* is represented only by *A. colubrina* var. *Cebil*. The original material is *Hassler 8348*, from salty sand near Bellavista, Paraguay (A, BM, C, MO, NY, US). It may be significant that the arrangement of inflorescences in racemose patterns, which is relatively uncommon for *A. colubrina* var. *Cebil,* should crop up in a specimen from a saline habitat. Such a locality is unusual for this variety but may be characteristic for the coastal *A. colubrina* var. *colubrina.*

Piptadenia macrocarpa var. *plurifoliata* (1919) Hoehne was to have been distinguished from *P. macrocarpa* var. *macrocarpa* by being a taller tree, over 20 m. high, by having more pinna pairs per leaf, 20-35, and by the different dimension of the heads, which were said to be 3 mm. in diameter in anthesis. Only the incredibly small size of the heads is outside the usual range found in *Anadenanthera colubrina* var. *Cebil.* The measurement published must be in error. The heads were said to be fasciculate in the leaf axils. Hoehne neither cited the original material nor indicated where it was collected, apparently in Brazil. I have been unable to locate the type but believe that the tree referred to cannot differ significantly from *Anadenanthera colubrina* var. *Cebil.*

Piptadenia microphylla Bentham (1841) was placed in the synonymy of *P. macrocarpa* by Bentham himself (1874-75). The original description noted the anther glands and cited the type material as " — Brazil, Sellow, Pohl." I have examined one sheet of Sellow, without a number, from Brazil (K), belonging to *Anadenanthera colubrina* var. *Cebil.* I do not know whether it is from the collection examined by Bentham, but it is possible to prove by another means that *Piptadenia microphylla* is synonymous with *Anadenanthera colubrina* var. *Cebil.* At the time that Bentham described *Piptadenia microphylla,* he was under the impression that all of the species now included *Anadenanthera* had the heads fasciculate in the leaf axils and subterminal. Surely, he would have mentioned as an important character the arrangement of inflorescences in paniculate patterns in the branch apices, had they been so in the type of *Piptadenia microphylla.* Furthermore, the pinna pairs are given as 20-30 per leaf for *P. microphylla.* Those of *Anadenanthera colubrina* var. *colubrina* do not exceed 25, whereas those of *A. colubrina* var. *Cebil* go to 35. The leaflets of *Piptadenia microphylla* are given as 50-80 pairs. Those of *Anadenanthera colubrina* var. *colubrina* are 40-60 pairs whereas those of *A. colubrina* var. *Cebil* range from 20 to 80 pairs per pinna. Finally, the original material was described as canescent-tomentellose, a condition more likely to be associated with *A. colubrina* var. *Cebil.*

Piptadenia Hassleriana was described by Chodat in 1904. The type material, which I have examined, was cited as *Hassler 6641,* flowering (A, NY, S and a photo from F) and *6641a,* fruiting (A, NY, S), both from woods in the Cordillera de Piribebuy, Paraguay. The description and the specimens agree with *Anadenanthera colubrina.* The tree in question was relatively small, 6-8 m. high. The pods were said to be not at all nitid. However, they were not scurfy or verrucose. Their small size and unusually fine reticulation may have made them less shiny than is common. The heads were described as glabrous but proved to be puberulous, at least in the bud. Chodat added that *Piptadenia Hassleriana* had affinities with the species here called *Anadenanthera peregrina,* differing from it by having glandular anthers. It is strange that he did not notice its closer relationship to *A. colubrina*. Although the tree described is small and has puberulous flower buds, the pinna pairs are 25-35, the leaflets 60-68 pairs, the petiole gland midway up the petiole, and the other glands 4-7, one between each of the ultimate pinna pairs. Hence, it is better placed in *Anadenanthera colubrina* var. *Cebil* than in the type-including variety. The locality of the collection is outside the known range of *A. colubrina* var. *colubrina*.

Piptadenia Hassleriana var. *fruticosa* was based on *Hassler 6688* from among barren cliffs in the valley of the Y-acá River, Paraguay (NY). I have examined this material, which is both flowering and fruiting. Having glandular anthers, it belongs to *Anadenanthera colubrina*. The plant is shrubby, 1-2 m. high, with 10-24 pinna pairs, 40-50 very small leaflets, .9-1.1 mm. long, and small heads. The absence of the distinctive characters associated with *A. colubrina* var. *colubrina*, and the fact that the material was collected in a region where, to my knowledge, only the other variety is found necessitates placing this unusual specimen in the all-accommodating *A. colubrina* var. *Cebil*. It may be that representatives of the characteristically variable *A. colubrina* var. *Cebil* respond radically to certain environments.

Shrub to tree, up to 30 m. high. Petiole gland more or less flattened, up to 5 mm. long; 1-3 (rarely to 7) smaller glands borne between the ultimate pinna pairs. Pinna pairs up to 35 or more, each pinna 1.2 or more cm. long. Leaflets 20-80 pairs, .9 or more mm. long, often dilated in the middle. Venation with the secondary reticulated veins prominent. Heads up to 20 mm. in diameter, including stamens, in fascicles of 1-4, more or less glabrous in the bud; the heads axillary to the leaves and subterminal, or sometimes borne in racemose patterns in the branch apices. Legume 10 or more cm. long, up to 3 cm. wide, margins strongly thickened; yellow-green in fresh, immature material. Seeds 8 or more, up to 20 mm. in diameter.

DISTRIBUTION. Herbarium specimens indicate that *Anadenanthera colubrina* var. *Cebil* occurs in Argentina (Catamarca, Corrientes, Jujuy, Misiones, Salta, Tucumán), Bolivia, Brazil (Bahia, Ceará, Maranhão, Matto Grosso, Minas Geraes, Pernambuco, Piauhy, Rio de Janeiro, São Paulo), Paraguay and Peru. Sometimes cultivated, this variety is common to *campos* or fields, where it is solitary. It is also found in wooded fields, along rivers, by lakes, in riverside forests; in salty sand; on dry slopes, rocky hills, high woods on foothills; and in mountain regions in riparian localities. It is found up to altitudes of 2100 m.

Several seedlings, introduced into Orlando, Florida, from São Paulo, Brazil, in 1940, have matured into large trees. They are probably the only living representatives of *Anadenanthera colubrina* in the northern hemisphere. They were to have been cut down in the spring of 1961, when the property on which they were standing was to have changed hands.

REPRESENTATIVE SPECIMENS. **Argentina. Corrientes:** *Meyer 2.122* (GH). **Jujuy:** *Lillo 11034* (F, U); *Venturi 5362* (F, US), *9730* (A, GH, MO, US). **Salta:** *Rodriguez 1101, 1107* (NY); *Venturi 8687* (US). **Tucumán:** *Venturi 1006, 1027* (A, US), *5455* (A, BM, S). **Bolivia:** *Steinbach*

6657 (A, BM, F, S), *7226* (A, BM, F, MO, NY, S, U). **Brazil. Minas Geraes:** *Glaziou 12653* (A, C). **Pernambuco:** *Pickel 3133* (F, GH, S, US), *4A.20M-12-16-29* (F, GH, MO, US). **Paraguay:** *Anisits 1958* (S); *Balansa 1419* (P, S); *Fiebrig 119* (A, F, L); *Hassler 3304* (A, BM), *7460* (A, C, MO, NY, S), *7600* (A, C, NY, S), *10657* (BM, K, MO, NY, S), *12230* (A, BM, C, F, GH, L, MO, NY, S, US), *12281* (A, BM, C, GH, L, MO, NY, US), *12309*, *12320* (A, BM, C, GH, L, MO, NY, S, US); *Jorgensen 4405* (A, C, F, MO, NY, S, US); *Lindman A2057* (GH, NY, S, US); *Malme 1096* (S). **Peru:** *Macbride & Featherstone 1353* (F), *2421* (F, US); *Weberbauer 6686* (F, GH); *J. West 3679, 3845* (GH, MO).

Anadenanthera colubrina var. *Cebil* may be distinguished from *A. colubrina* var. *colubrina* by the following characters: it is a taller tree. The petiole gland tends to be longer but flatter. The pinna pairs may be more numerous but the pinnae shorter than in the other variety. The leaflets tend to be more numerous, shorter and more often dilated in the middle, with the secondary reticulated veins prominent. The heads may be larger than in var. *colubrina;* they are not whitish in the bud, and the annular involucre is not easily visible below them at that time. In addition, the heads of var. *Cebil* are usually axillary to the leaves and subterminal, and less frequently borne in racemose patterns in the branch apices with the subtending leaves reduced. The legume is shorter and wider than that of var. *colubrina*, not as regularly contracted and with thicker margins. The seeds are fewer and larger. *Anadenanthera colubrina* var. *Cebil* is much more variable than is var. *colubrina*. Specimens examined show var. *Cebil* to be found today from near the equator to about 30 degrees S. latitude, overlapping geographically with the distribution of var. *colubrina*.

Excluded Names

Bentham suggested (1874-75) that *Acacia grata* Willdenow, "ex diagnosi nimis brevi", might be the same as what he called *Piptadenia macrocarpa*. In 1919, Macbride stated that *P. macrocarpa* seemingly had not been given its first specific designation and that the epithet *grata*, published in 1809, might be available for it. The type material of *Acacia grata, Hoffmannsegg s. n.*, "Habitat in Brasilia", is no longer extant in Willdenow's herbarium at Berlin, and I have been unable to locate a photograph of it. Furthermore, Macbride has informed me (in a letter, April 20, 1959), regarding his earlier proposal, that ". . . probably the new combination was made as was the custom at one time on a statement of some previous investigator, or maybe simply on the statement of Index Kewensis . . . It is possible that Harms verified the status of *grata* as he was curator for many years at the Dahlem Herbarium". Harms is no longer living, and Brenan suggested in 1955 that it would be unwise to replace *macrocarpa* with an epithet of such uncertain application. *Acacia grata* is the name-bringing synonym for *Mimosa grata* (Willd.) Poiret, published in 1817 without adding any new information. In the absence of any further evidence as to the identity of *Acacia grata*, it seems best not to include that name in the synonymy of *Anadenanthera colubrina* var. *Cebil*.

Mimosa angustifolia Lamarck (1783) was treated with a questionmark by DeCandolle, as possibly synonymous with *Acacia angustiloba* DeCandolle, which is a synonym of *Anadenanthera peregrina* var. *peregrina*. Lamarck's original description appears to have been based on two sources of information. One of these was Nicolson's description of *Tendre a caillou franc* (1776), which was not accompanied by a Latin binomial and cited no material. The other source was nonflowering living material that Lamarck had seen, probably that which he mentioned as in cultivation in the "Jardin du Roi". The tree was said, by Lamarck, to grow in Saint-Domingue, now known as Hispaniola. I have obtained photographs of two sheets labelled *Mimosa angustifolia* from Lamarck's herbarium in Paris. These specimens, one in flower (No. 116-316) and one in fruit (unnumbered), most likely were taken from the tree in cultivation. The flowering example, if not the other, must have been acquired by Lamarck after the publication of the original description in which he stated he had not seen the flowers. Although their specific identity cannot be established with certainty from photographs, the two specimens appear to coincide in their characters with the description of Lamarck. But neither they nor the description conforms to the characteristics of *Anadenanthera peregrina*. The flowering specimen bears inflorescences "en grappe", the heads being clustered in a terminal paniculate pattern, as reported from Nicolson by Lamarck. The pinna pairs per leaf on the flowering specimen are barely 10, which is more than the 4-5 on the fruiting specimen and in Lamarck's description. The leaflets are very distinctly dorsiventral. The fruits on the second specimen are small, apparently thin and membranaceous. According to the descriptions of Nicolson and Lamarck, they are also yellowish. Specimens that I have seen identified as *Mimosa angustifolia* Lamarck lack flowers but are otherwise distinctive (*E. C. Leonard & G. M. Leonard 12617*, Haiti; *E. J. Valeur 462*, Dominican Republic; both from A). The seeds are not dissimilar to those of *Anadenanthera peregrina* but have narrower rims and tend to be more oblong, as well as fewer in number. The pods are slightly lustrous and not scurfy to verrucose. The pinna pairs are at the most 12 per leaf. Without flowering specimens for examination, I would not want to speculate upon the identity of the material involved in this problem. However, I am sure that *Mimosa angustifolia* does not belong to the genus *Anadenanthera*, as here interpreted.

Another species of Lamarck that must be considered here is *Mimosa filicifolia* (1783), which that author described from vegetative parts only and, in his own words, "par présomption" suggested that it might be the same as *Mimosa peregrina* L. Lamarck cited no material. The description alone is inadequate to identify it from among probably half of the species of the *Mimosoideae*. In 1844, Bentham transferred *Mi-*

mosa filicifolia to the genus *Pithecellobium* Mart. He had by then described the genus *Piptadenia.* Lamarck's description of *Mimosa filicifolia* and Bentham's description of *Pithecellobium filicifolium* differ somewhat as to the numbers of pinna pairs per leaf and of leaflets per pinna. Bentham did not indicate, either, whether he had seen Lamarck's material. Specimens which I have seen labelled *Pithecellobium filicifolium* in the Gray Herbarium come from Mexico and Central America, where none of the Anadenantheras is known to occur (*E. Langlassé 103, E. W. Nelson 2671, C. A. Purpus 8251,* all from Mexico; *Tonduz 12503,* from Costa Rica). The specimens examined appear to be somewhat variable in numbers of foliage parts, approaching more closely the measurements given by Bentham. Both the descriptions, and the specimens examined, show fewer pinna pairs and fewer leaflets than is common for *Anadenanthera peregrina.* The leaflets also are larger. The heads are large by comparison, and the flowers are of a different structure. On the basis of the specimens seen and evidence from the literature, *Mimosa filicifolia* cannot properly be included in the synonymy of either species of *Anadenanthera.*

The name *Acacia trichophylloides* Macfadyen was published in 1837, with a rather detailed description but without citing specimens. Later, Grisebach (1859-64) treated it as a synonym of *Acacia Julibrissin* Willdenow. He had seen Macfadyen's material and apparently distinguished it from *Piptadenia peregrina,* which also appeared in the same publication. Some time afterwards, Bentham (1874-75) stated that Macfadyen's description of *Acacia trichophylloides* was at variance with what he referred to as *Albizzia Julibrissin* but that it agreed well with *Piptadenia peregrina.* I have not seen Macfadyen's material, but his description differs from *Anadenanthera peregrina* by referring to a smaller tree with angulose and purple branch extremities. The leaves are apparently much shorter and the pinna pairs many fewer than in *A. peregrina.* The ovary is reported to be white-villous with appressed hairs, a condition never found in *Anadenanthera.* Bentham may have been misled by the fact that Macfadyen gave *Acacia angustiloba* DeCandolle (1825), as a synonym of *A. trichophylloides,* for Bentham knew *A. angustiloba* to be synonymous with *Piptadenia peregrina.* The herbarium specimens that I have seen of *Albizzia Julibrissin* from the West Indies are without flowers, but Macfadyen's description of *Acacia trichophylloides* more closely resembles these specimens than it does those of *Anadenanthera peregrina.*

Schleinitzia microphylla?

Outside of the New World, only one species attributed to the *Piptadenia* complex has been described with a truly capitate inflorescence. Now usually referred to as *Piptadenia novo-guineensis,* it was originally described in the monotypic genus, *Schleinitzia,* as *S. microphylla* Warburg (1891). The collection upon which the description was based was *Hollrung 598;* the type was destroyed at Berlin in 1943, and a duplicate at Breslau presently is unavailable for loan. The collection was made near Finschhafen, New Guinea. In describing *Schleinitzia,* Warburg stated that, although the tree was closely related to *Piptadenia,* as Bentham interpreted it, the presence of glands on only 5 of the 10 anthers provided the basis for treating the species in a separate genus. Not long afterward, Warburg (1891) decided that *Schleinitzia* might better be united with *Piptadenia* on grounds that the number of anther glands was a variable character not well known in *Piptadenia*. The epithet *microphylla* was dropped because it already had been applied to a species of *Piptadenia*. Warburg added that, unless a new section were created to accommodate *P. novo-guineensis*, the species would have to be placed in the exclusively American section, *Niopa*.

A new section has not been published for that species, to my knowledge, and *Piptadenia novo-guineensis* has been mentioned rarely in the literature. The fact that the species is not American is a relatively weak objection to placing it in *Anadenanthera*. However, this species differs from the members of *Anadenanthera* by having a distinctly septate pod which dehisces along both sutures, and seeds which are lenticular to obovate. Furthermore, the specimens examined are variable as to the presence or absence of anther glands even from flower to flower upon single heads. Usually, there are at least 5, commonly more and up to 10, anther glands in the bud. *Piptadenia novo-guineensis* resembles the species of *Anadenanthera* in habit, foliage, inflorescences and arrangement of inflorescences. But it is found under different ecological conditions, forming a characteristic element of the tropical rain-forest. The leaflet of this species, as seen in Plate XI, can be distinguished from that of *Anadenanthera* by the presence of three veins, instead of one, arising from the base of the leaflet. Furthermore, the wood of this species differs markedly in appearance, weight, etc., from that of *Anadenanthera*, according to Brazier (1958), who doubts that the species would be placed correctly in the *Piptadenia* complex. Finally, there is no indication from any source that this species is included in native pharmacopoeias, unlike the species of *Anadenanthera*.

Collections of *Piptadenia novo-guineensis* from New Guinea, Rossel Island and two of the Solomon Islands, Bougainville and San Cristoval, show the species to be represented as an erect, thin, tall tree, 5-20 m. high, with open and spreading branches, and sensitive, pale green leaf-

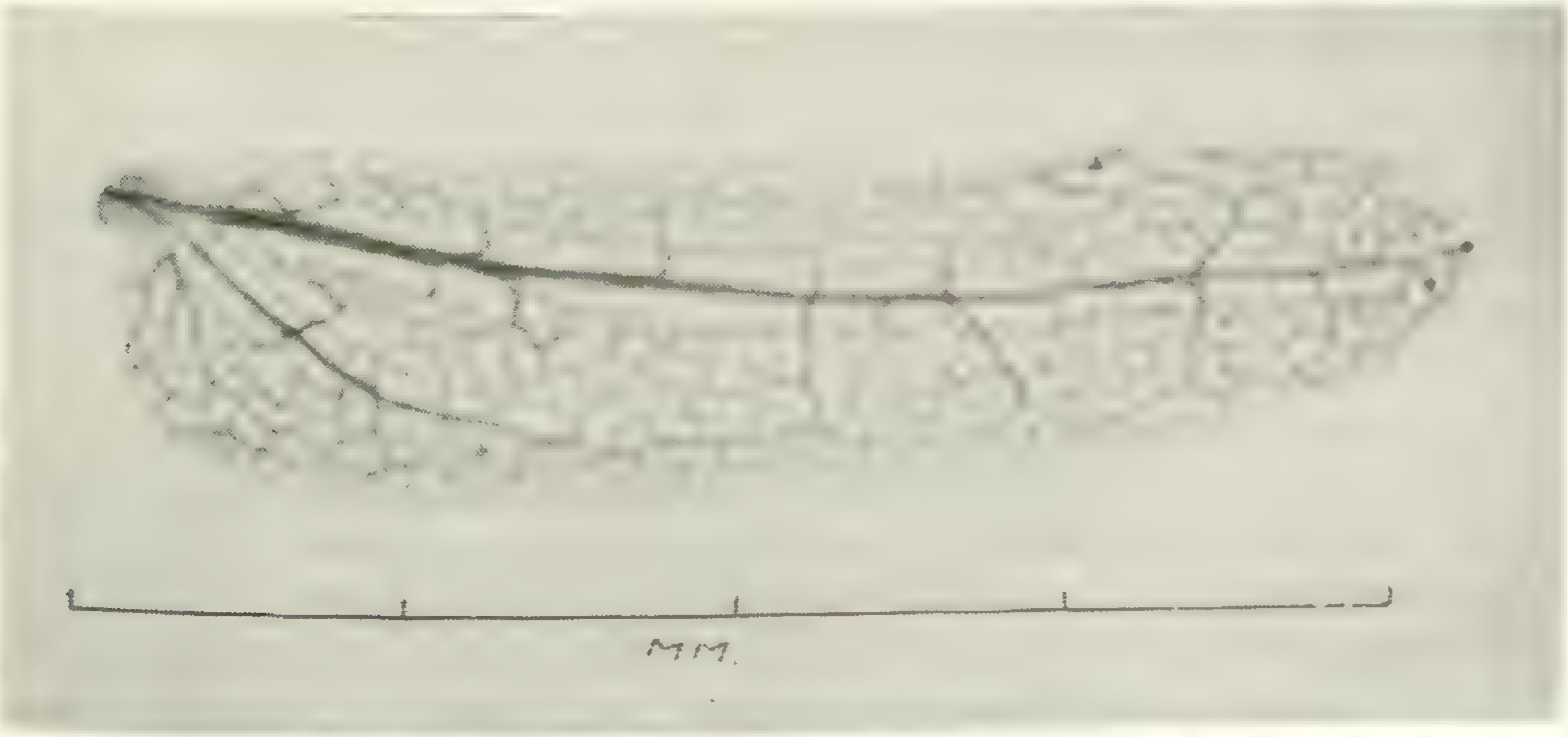


PLATE XI. Cleared and stained leaflet of *Schleinitzia microphylla*. Note the three veins arising from the base of the leaflet (*L. J. Brass 2738*, San Cristoval I.).

lets. The bark is 1-4 mm. thick, whitish gray to purplish brown, with many broad, shallow longitudinal fissures in which are numerous transverse, light brown lenticels exuding an amber gum. The sapwood is 2 cm. deep and straw-colored. The heartwood is gray-brown (compared to reddish in *Anadenanthera*). The diameter of the trunk may reach 27 cm. in large individuals. The profuse flowers appear to be pale pink or cream-colored or white from a distance, due to the pink or purple filaments, which become whitish in older flowers. The anthers are yellow. The young fruits are red-brown, the mature ones dark brown or black. The tree is found in secondary growth of coastal rain-forests at altitudes up to 250 m. It has been reported also as fairly common in savanna or coral-limestone in the coastal plains up to 5 m. altitude.

Specimens examined from Guadalcanal in the Solomon Islands represent the first in a series from the New Hebrides, New Caledonia, the Fiji Islands, Cook Islands and the Society Islands, all of which have been identified by previous botanists as *Leucaena Forsteri* Bentham (1842) or one of its synonyms. Bentham did not designate a type for this species. Of its two synonyms, *Mimosa glandulosa* Forster (1786) is a *nomen nudum*, and *Acacia insularum* Guillemin (1837) is not typified.

These specimens from the eastern islands exhibit variation in: the form, relative size and pubescence of the leaflets; the overall pubescence of the foliage; the presence or absence and location of foliage glands; the relative thickness and length of the peduncle; the position of the annular involucre upon the peduncle; the structure of the bract which immediately subtends each flower in the head and which may be filiform to broad at the base and sometimes extends into a point above the unopened bud; the relative length of the calyx; the degree of coherence and the basal width of the petals; the size and shape of the anthers, whose chambers appear to be winged in some specimens (perhaps due to shrinkage in drying); the presence or absence of anther glands; the fruits, which range in color from reddish brown to black and may be pointed or rounded at the apex.

When Bentham defined *Leucaena* in 1842, he recognized the similarities in habit and appearance between it and section *Niopa* of *Piptadenia*. On the basis of characters enumerated by Bentham, plus my own observations of herbarium specimens of the genus, *Leucaena* appears to differ from *Anadenanthera* by having heavier peduncles, larger heads and flowers, basally narrowed and distinctly free petals, sometimes pilose but always eglandular anthers, and lenticular seeds which are borne in a smooth pod that dehisces along both sutures.

Leucaena would seem to be distinguishable from *Piptadenia novoguineensis* by the same floral characters by which *Leucaena* is separated from *Anadenanthera*, and by having a unilocular fruit. The lenticular seeds of *Piptadenia novo-guineensis* are similar to those of *Leucaena* and to those of the genus *Pityrocarpa* as interpreted by Brenan in 1955; but the consistency of the pod of *Piptadenia novoguineensis* is more like that of *Leucaena*, being less membranaceous than that of *Pityrocarpa*.

In view of the relative distinctness of the taxon now being called *Piptadenia novo-guineensis*, it would not be unrealistic to recognize it as a genus separate from *Piptadenia*. In that case, it should be known as *Schleinitzia microphylla* Warburg.

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INFRASPECIFIC VARIATION IN THE GUTIERREZIA SAROTHRAE COMPLEX (COMPOSITAE-ASTEREAE)

Otto T. Solbrig[1]

The understanding of morphological variation in organisms is of fundamental importance for the student of systematics and has received increased attention over the last fifty years. The presence of an array of diverse genotypes in a population allows evolutionary adjustments to environmental changes, and phenotypic differences to a certain extent reflect the amount of genetic variation in a species population. Yet phenotypic differences are not only governed by the theoretical or actual presence of a large number of different genotypes, but depend also on the buffering or "homeostatic" properties of the individual and the population, genetic homeostasis being apparently governed by the amount of heterozygosity in the gene pool of a population. The breeding system also plays a very important role in the amount and type of phenotypic variability present. Another important factor is the spatial relationship of the individual in the population, which will govern the amount of inbreeding vs. outbreeding in self-compatible plants, or influence the rate of recombination in self-incompatible species. Needless to say, breeding systems and especially the actual amount of outbreeding are important determining factors of the type and amount of variation in a population of plants.

Differences between populations can be due to a series of factors. The best-known is geographical variation correlated with environmental change. In such cases the differences can have a genetical basis as a result of different selection forces in response to changed conditions, or they may be the result

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[1] This work is an outgrowth of studies made in connection with my revision of the North American species of *Gutierrezia* (Solbrig, 1960) and of studies of the South American species of the genus currently in progress. In the course of its realization many persons have helped in many ways. Particularly I want to thank Miss Julia Barth, Mr. John Chittum, Dr. and Mrs. Vladimiro Ern, Dr. Peter Raven, Mrs. Lily Rüdenberg, and Ing. Agr. Benno Schnack. Dr. Reed C. Rollins read the manuscript and made valuable suggestions. Field work in the United States and Mexico over the last five years in connection with this project, was made possible through generous grants from the American Academy of Arts and Sciences, Boston; the Associates in Tropical Biogeography and the "Patent Fund" of the University of California; and the Fund for Evolutionary Biology at Harvard University. A grant from the National Science Foundation made field work in South America possible, and aided in other ways. To all I express my sincere appreciation.

of different canalizations of development resulting from the altered environment. Other factors accounting for variation between populations are accidents of colonization in the expansion stages of a species, and in small populations chance elimination of certain genotypes from the gene pool.

Unfortunately it is not always possible to tell in natural populations even after a detailed investigation, what the true genetic component of variability is, and a reasonable approximation is usually the best that can be hoped for. The experimental methods demanded to obtain even an approximate knowledge of the hereditable component of variation are not successfully applicable to all types of material and require, at best, several generations of breeding as well as the culturing of large progenies before satisfactory results can be obtained. Therefore, experimental procedures are not always to be recommended, for example with perennial plants where a long generation period is involved.

Even where a detailed analysis is not possible, a certain understanding of the pattern of variation is a necessary requirement for the student of evolution and the taxonomist alike. Different genotypes may give rise to similar phenotypes under a particular environmental condition, due to the phenomenon of "genetic homeostasis" as indicated above; furthermore, under different environmental situations, similar genotypes may give rise to dissimilar phenotypes due to genotypic plasticity. Therefore, it is obvious that measurements of phenotypic characters cannot be taken as necessarily reflecting directly the nature of the genotypes. Nevertheless, natural selection affects phenotypes and only indirectly genotypes and, furthermore, the systematist interested in the affinities and relationships of plants has by necessity to concern himself with phenotypic relationships. From this point of view, attempts to study variability of the phenotype without a knowledge of the genetic and developmental bases are justified. Such studies are usually an integral part of any taxonomical work, although their accuracy and the amount of detail possible vary appreciably. The present study is of the latter type.

Gutierrezia sarothrae is a perennial globose subshrub relatively common in western North America west of the Great Plains. It extends from northern Mexico to southern British Columbia and Alberta in Canada. The plants are

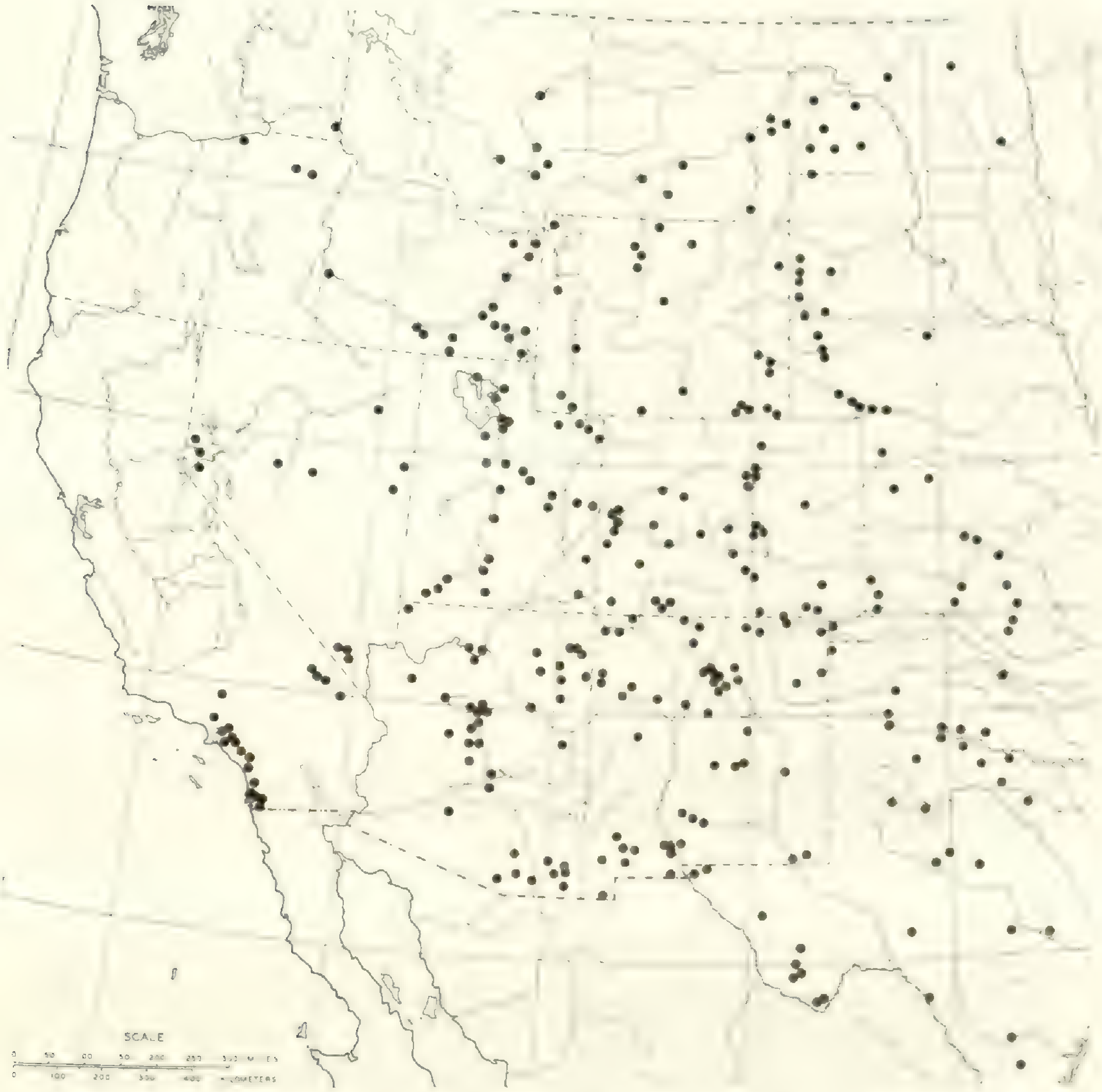

Fig. 1. Distribution map of *G. sarothrae* in the United States. Goode Base Map copyrighted by the University of Chicago.

found growing in populations which have usually between 50 and 500 densely aggregated plants, although occasionally populations of up to several thousand plants are found. The species is most abundant in the Rocky Mountain area, and adjacent plains, below 2000 m., in the valleys of the major drainage systems and neighboring regions, such as the Colorado, Snake and Missouri river valleys. It is almost entirely absent from the Sonoran, Mohave and Great Basin desert areas, but is found on the western edge of this zone in southern and Baja California, around Reno, Nevada, and in eastern Oregon and Washington (fig. 1). Over this area populations of *Gutierrezia sarothrae* show a great deal of variation, as is to be expected. This fact is even more striking when the analysis is restricted to non-random samples, as herbarium specimens often are. Such a procedure has led to the description of 23 separate entities within this complex. Field studies have shown that the characters used to separate specimens in the herbarium show a continuous or almost continuous variation in the field, and "specific" characters are often found in different members of the same population, or even in different stages of the ontogeny of a single plant (Solbrig, 1960). One object of the present investigation has been to attempt to quantify and assess the morphological variation within and between populations of *G. sarothrae* and to attempt to establish and evaluate the relative importance of the factors that account for this variability. It is hoped that the information presented will help in understanding the evolutionary history of the species, and an attempt is made to relate it to the broader context of evolutionary theory.

A second very special aim of this study has been to see if any quantitative differences can be discovered between the diploid and tetraploid races of *Gutierrezia sarothrae*. As was shown elsewhere, (Solbrig, 1960), there are no qualitative differences between the two levels of ploidy. In view of the fact that qualitative and/or quantitative differences were observed in the majority of the studies of polyploidy done to date, particularly those dealing with artificial tetraploids, the situation merits special consideration.

The methods of investigation chosen, detailed measurements of random samples of populations, observations of greenhouse cultures, together with cytological studies, are believed to be the ones that are the most efficacious in producing useful data in the present situation. Techniques often used in the study of variation in annual plants, particularly crossing experiments, are unprofitable in the case of relatively large, self-fertile, perennial plants that require extensive greenhouse facilities and a minimum of a year between generations. These techniques have been applied randomly or not at all.

CHROMOSOME STUDIES[2]

Chromosome number has been determined from anther squashes, and root tip squashes in 59 populations (table 1).

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[2] I am particularly indebted to Mrs. Lily Rüdenberg who prepared the slides used for the studies of chromosome morphology, and who also obtained some of the meiotic counts.

Forty-nine populations proved to be diploid with n = 4, while the remaining 10 were tetraploids with n = 8. Meiosis was regular, and such irregularities as could be detected (occasional "sticky" bridges, and rare univalents) were present in low frequency and appear to be of no significance. One population from Texas had two supernumerary chromosomes, which are apparently eliminated in the microgametophyte by formation of microsporocytes during meiosis.

In order to determine whether there were any differences between populations in respect to the gross arrangement of the chromosomal arms by which populations could be cytologically identified, a study of root tip chromosome morphology was made. Plants of seven populations were investigated, grown from seed gathered at Dickinson, North Dakota (3244), Sheridan, Wyoming (3252), Evanston, Wyoming (3257), Dubois, Idaho (3254), Thompson, Utah (3260), Fountain, Colorado (3264), and Altus, Oklahoma (3289). The results of the study were largely negative, since no differences in the chromosome morphology of these populations could be detected. However, the data for a description of the karyotype of *Gutierrezia sarothrae* were obtained (Rüdenberg & Solbrig, 1963).

The chromosomes of *Gutierrezia* are small, and therefore no attempt was made to measure arm length in the various populations, since the probable error would doubtless be too great to give meaningful data. Nevertheless the four chromosomes of *G. sarothrae* are qualitatively different and can be identified with relative ease. The centromere of one pair is median, while the position of the centromere in the other three pairs is subterminal. Since the median chromosome is

FIG. 2. Metaphase plate of root tip mitosis and chromosome idiogram of *G. sarothrae*.

TABLE 1. CHROMOSOME NUMBERS DETERMINED IN POPULATIONS OF G. SAROTHRAE

A. n = 4

NORTH DAKOTA. 12 mi. N. of Belfield on Hwy. 85. *Solbrig 3245.*
MONTANA. 3 mi. E. of Sanders. *Solbrig 3250.*
SOUTH DAKOTA. Hwy. 385, on the N. & S. Dakota border. *Solbrig 3240.*
Hwy. 16, 10 mi. N. of Rapid City. *Solbrig 3236.*
WYOMING. 17 mi. S.E. of Mountainview on road to Lonetree. *Solbrig 3134.*
Hwy. 30, 91 mi. W. of Evanston. *Solbrig 3257.*
Outskirts of Sheridan. *Solbrig 3252.*
IDAHO. 12 mi. E. of Dubois on road to Kilgore. *Solbrig 3254.*
OREGON. Field Creek. *R. Ornduff s.n.*
NEBRASKA. 1 mi. N. of Lisco on road to Orlando. *Solbrig 3228.*
2 mi. E. of Roscoe on road to Ogallala. *Solbrig 3224.*
KANSAS. 10 mi. S. of Medicine Lodge. *Solbrig 3292.*
COLORADO. 1 mi. W. of Hwy. 50, 22 mi. S. of Grand Junction. *Solbrig 3153.*
Colorado Nat. Mon., 1 mi. N. of Campground. *Solbrig 3262.*
Fort Collins. *A. Weber s.n.*
UTAH. Hwy. 24, 15 mi. S. of Jct. with Hwy. 6. *Solbrig 3151.*
Hwy. 54, 7 mi. S. of Boulder. *Solbrig 3150.*
Red Canyon, just before Bryce Canyon Nat. Park. *Solbrig 3145.*
Diamond Valley, Diamond Mt. Rd., 16 mi. S.E. of Jct. Hwy. 44. *Solbrig 3136.*
Hwy. 44, 16 mi. N. of Vernal. *Solbrig 3258.*
Hwy. 50, 4 mi. W. of Thompson. *Solbrig 3260.*
Wasatch Mts. *R. K. Vickery Jr. s.n.*
OKLAHOMA. 4 mi. E. of Clinton, Hwy. 66. *Solbrig 3290.*
TEXAS. Hwy. 62, 11 mi. W. of Altus, Okla. *Solbrig 3289.*
Hwy. 67, 7 mi. E. of Alpine. *Solbrig 3280.*
Hwy. 254, 5 mi. W. of Craford. *Solbrig 3287.*
Hwy. 277, 5 mi. W. of Abilene State Park. *Solbrig 3286.*
Hwy. 67, 12 mi. W. of San Angelo. *Solbrig 3283.*
Hwy. 62-180, 23 mi. S. of White City, N. M. *Solbrig 3271.*
NEW MEXICO. Hwy. 62-180, 3 mi. S. of White City. *Solbrig 3270.*
Hwy. 285, 20 mi. N. of Roswell. *Solbrig 3269.*
Hwy. 20, 12 mi. S. of Ft. Sumner. *Solbrig 3267.*
ARIZONA. 12.6 mi. E. of Ash Fork. *Solbrig 2801.*
0.8 mi. E. of Hyde Park. *Solbrig 2805.*
CALIFORNIA. 12.3 mi. W. of Aguanga. *Solbrig 2760.*
9.9 mi. S. of Santa Ysabel. *Solbrig 2763.*
2 mi. W. of Temecula. *Solbrig 2758.*
9.8 mi. S. of Santa Ysabel. *Solbrig 2765.*
1.6 mi. W. of Rancho Santa Fe. *Solbrig 2769.*
8.5 mi. E. of Chula Vista. *Solbrig 2766.*
6.2 mi. E. of Chula Vista. *Solbrig 2768.*
11.1 mi. E. of Idyllwild. *Solbrig 2773.*
NEVADA. Virginia City. *R. H. Miller s.n.*
Mt. Rose. *R. H. Miller s.n.*

B. n = 8

SOUTH DAKOTA. Hwy. 385, 8 mi. S. of Oelricks. *Solbrig 3233.*
COLORADO. ½ mi. before W. entrance to Colorado Nat. Mon. *Solbrig 3261.*
TEXAS. Hwy. 80, 11 mi. W. of Van Horn. *Solbrig 3212.*
  Hwy. 67, 6 mi. W. of McCamey. *Solbrig 3282.*
  Hwy. 54, 30 mi. N. of Van Horn. *Solbrig 3273.*
NEW MEXICO. 3 mi. S. of Jct. Hwy. 285 & 286. *Solbrig 3169.*
ARIZONA. 5 mi. N. of Payson. *Solbrig 2794.*
  9.8 mi. W. of Seligman. *Solbrig 2802.*
  19.8 mi. N. of Roosevelt Dam. *Solbrig 2792.*
  Jct. Payson-Phoenix & 488 Hwys. *Solbrig 2793.*

also the shortest, it can easily be identified in root tips (No. IV in the diagram, fig. 2). The short arm of one of the other pairs is slightly longer than that of the other two. This characteristic, combined with the slightly shorter size of this chromosome as compared with the other subterminal chromosomes, makes this pair identifiable (No. III, fig. 2). Finally, the two remaining pairs can be separated by the presence of a secondary constriction (probably the nucleolus organizer) in one of them (No. I, fig. 2). The secondary constriction is located very close to the centromere, and is detected only in stages such as anaphase, when the chromosomes are not too contracted. The primary and secondary constrictions cannot always be told apart at metaphase, but due to a tendency for the satellite to break off easily when squashed hard (fig. 2), it is usually possible to tell the SAT chromosome, even in stages of maximum contraction.

Unfortunately no tetraploid plants were available for the study of chromosome morphology. Since the tetraploid plants are morphologically very similar to the diploids, an autopolyploid origin is suspected. In such a case a certain amount of multivalent pairing at meiosis might be taken as a confirmation of this view, but although a careful search was made, none was found. However, the finding of perfect diploid pairing in tetraploid plants does not necessarily rule out autopolyploidy, since pairing is apparently controlled by mendelian factors in at least some species (Lövquist 1956, Riley 1960, Johnson 1963). Another possibility is that these are segmental allopolyploids (Stebbins, 1950) or even true allopolyploids, although this last assumption is unlikely. (For more details see discussion under sibling and incipient species).

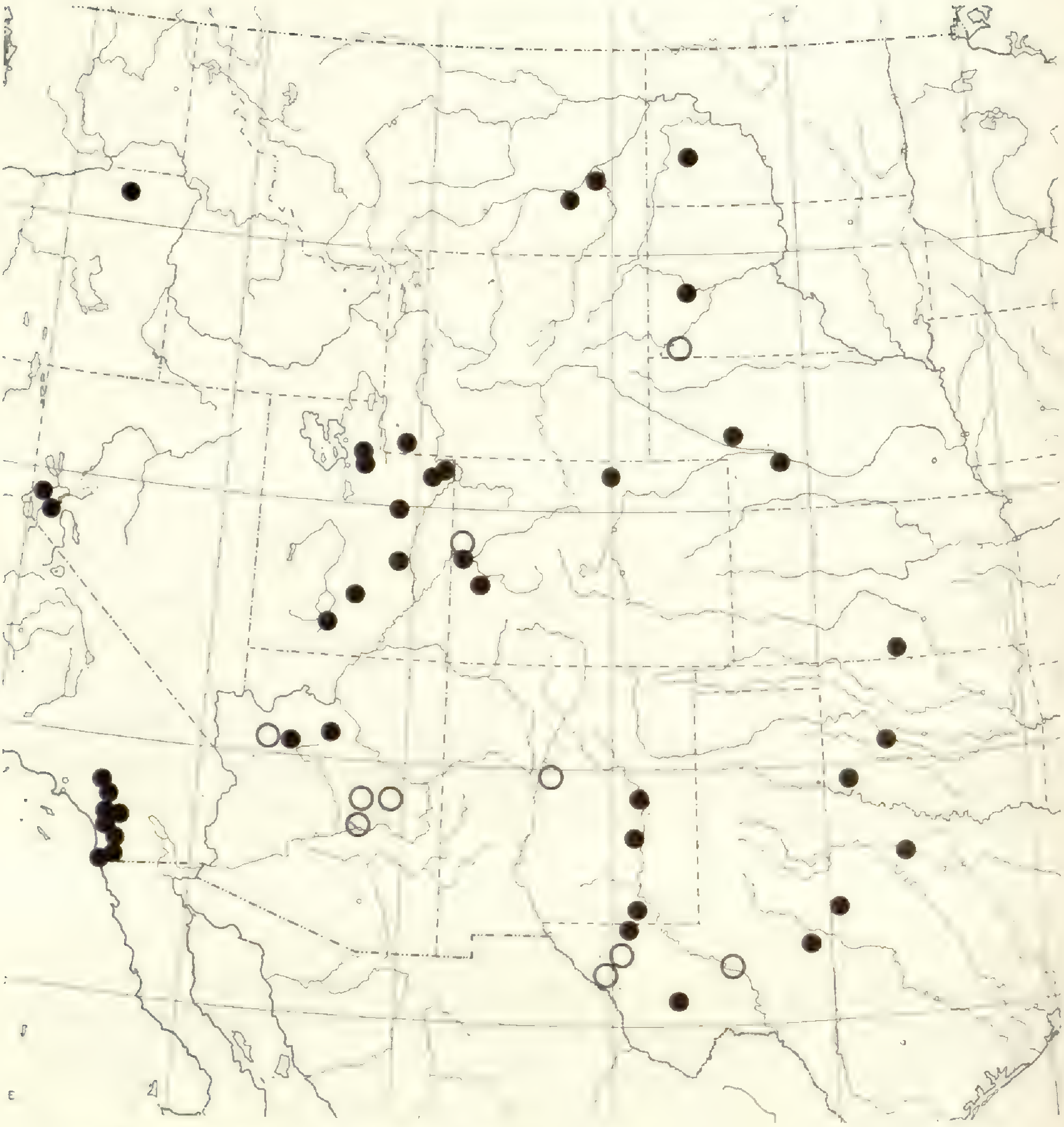

FIG. 3. Distribution of diploid (dark dots) and tetraploids (light dots) populations. Goode Base Map copyrighted by the University of Chicago.

STATISTICAL METHODS

This work is primarily based on an intensive study of 65 natural populations more or less randomly distributed throughout the range of the species (for exact localities see appendix). The principal data were obtained by measuring up to 11 characters in each of 50 plants chosen at random from each population.

In a study such as this one, involving a series of measurements, there are two major procedural problems: sample randomization and the choice of the statistical tests that will be most meaningful. An absolute prerequisite of any statistical work is making certain that no bias of any sort is committed when the basic information is being gathered. This is accomplished by randomization. We now have several techniques available, borrowed from statistics and ecology, which can be used to randomize a sample. Before adopting any of these, it is essential to find out their relative degree of accuracy, that is, to find out to what degree bias will be eliminated, and then to determine whether the added lack of bias in the data obtained by using more laborious methods will justify the extra work needed to obtain the more precise result. Whenever the added accuracy is less than the expected error from other sources, the limit beyond which no extra work is justified has been reached. Unfortunately, in the present investigation there was no way by which the total error due to sources other than sampling could be assessed (such as degree of phenotypic plasticity), and therefore an empirical test was used to assess the relative value of different sampling techniques. At first, samples were taken completely at random. This was accomplished by the use of a grid and a pair of dice (a table of random numbers would have been equally useful). Next, samples were obtained by walking diagonally through the population and choosing each tenth plant. Since there was no appreciable difference in the results, the second, less time consuming method was adopted for the remainder of the investigation.

The choice of statistical tests was a much harder problem. The major difficulty, of course, is that the nature of the data is being influenced by two major components: genotype and environment. If the usual statistical tests of significance are applied the level (usually 5% and 1%) at which the results are statistically significant or not can be learned. But such a statement is in my opinion not very meaningful biologically. *F* tests resulting from an analysis of variance indicate whether data can properly be considered to be from samples of the same statistical population. This information can be of use, but it is doubtful that this type of statistic has validity in the present instance, since the analysis of variance was developed for use with experimental data and not observational data. The main difference is that the present samples were produced under a variety of environmental conditions, and not under uniform or relatively uniform conditions as is usually the case. Significance tests (*t* tests) of the difference between diploids and tetraploids are valid, I feel, and they have been used. This is so because all the data gathered are lumped into two classes and the variable tested, chromosome number, is constant within each of the two categories. The standard deviation and standard error of the mean have been calculated for each character in each population. This is also a fairly straight-forward test of the amount of dispersion in each character measured in a population. Whenever possible an effort was made to represent the statistics in a graphic manner, and only the more obvious conclusions as to correlations were made.

STUDIES OF VARIATION

The following study of the morphological variation of *Gutierrezia sarothrae* is based upon some 30,000 measurements made on over 3,000 plants. The total number of populations for which there are herbarium samples is in the neighborhood of 5,000, and assuming an average of 100 plants per population (a rather low estimate), there are a minimum of 500,000 plants of *G. sarothrae* in nature. Probably a figure twice as large somewhat approaches the number of plants in nature, but it could easily be 10 times as large. Therefore our sample represents somewhere between 0.05 and 0.5% of all the plants.

Fifty-three natural populations (fig. 4) were sampled and measured. The samples were obtained at random (see statistical methods). The characteristics measured or counted were: plant height, height and width of the involucre, number of tubular and ligulate flowers, length of the pappus of the ligulate and tubular flowers, length and width of the achene of the tubular and ligulate flowers, pollen diameter and stomatal guard cell length. In addition, observations on blooming period were recorded in the greenhouse and in the field, and from herbarium specimens.

PLANT HEIGHT. Measurements were taken with a steel measuring tape, the height recorded is that from the base of the plant to the tip of the longest branch. All measurements of plant height are expressed in inches, since no metrically marked tape was available, and converting inches to centimeters would have introduced a source of inaccuracy. Height was measured in all 53 populations, the sample consisted of 50 plants in all but two populations; the sample in these two consisting of 35 plants, the total number of plants

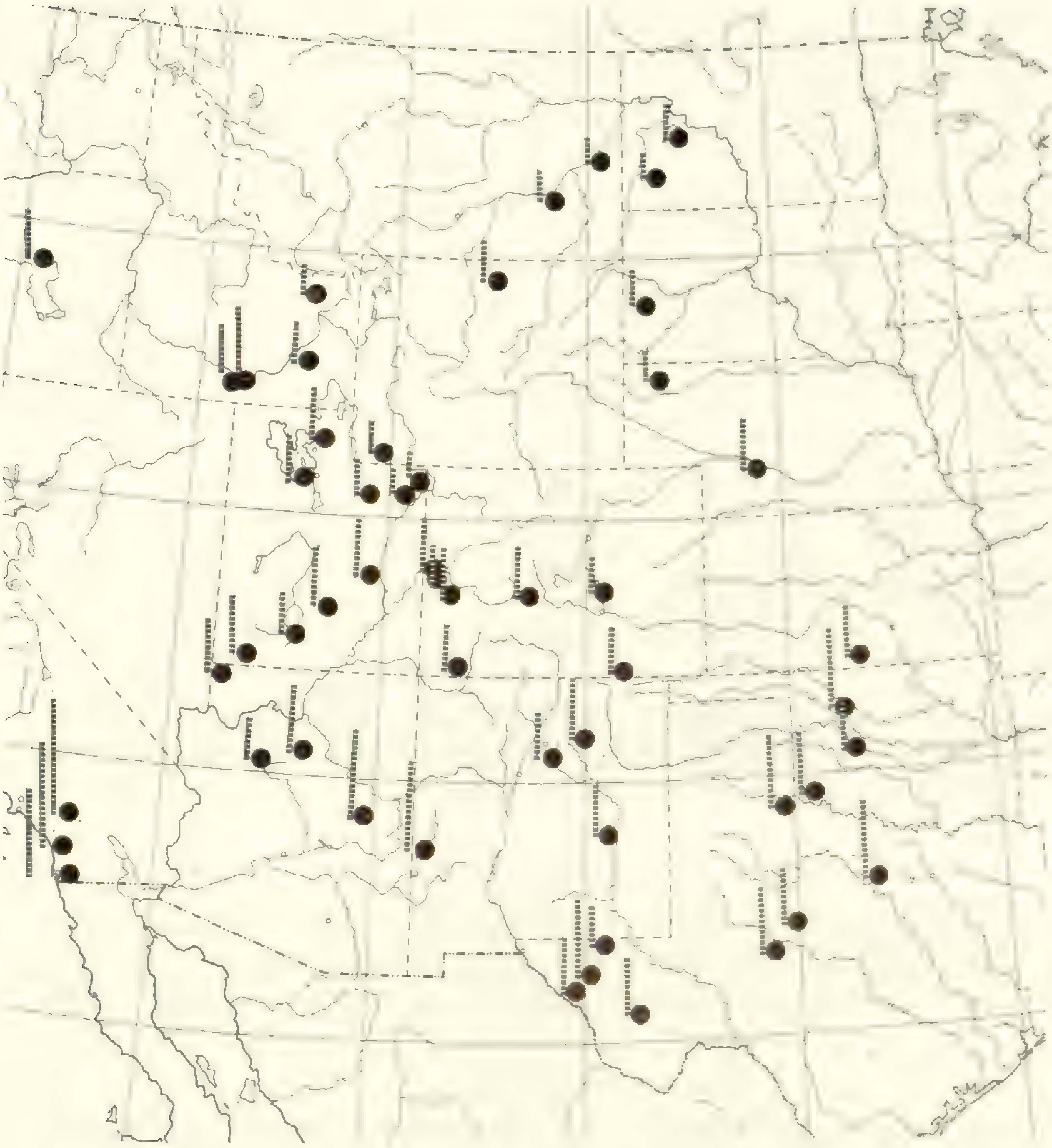

FIG. 4. Mean height of populations of G. sarothrae. Goode Base Map copyrighted by the University of Chicago. .

present. Plant height varied considerably both within and between populations. The largest single plant (38 inches) was over nine times as big as the smallest single plant measured (4 inches), while the average height of the tallest population (22.4 inches) was about 4.5 times higher than the shortest population. In spite of these differences the size distribution is continuous, both within and between populations (fig. 4, table 2). When grown in the greenhouse and/or the garden, plants from different populations attained different heights (some were up to 2.5 times as tall as others), while the plants from the same locality were relatively uniform. This suggests that the differences in plant height between populations are genetically controlled. On the other hand, the plants grown in the greenhouse were as a rule larger than the plants in the field, which in turn shows that there is a certain degree of unrealized potential under natu-

TABLE 2. MEAN, RANGE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR PLANT HEIGHT.

Coll. No.	$\bar{x}$ ± *St. error*	*Range*	*s*	*C(%)*	*n*
NORTH DAKOTA					
3243	5.48 ± 0.15	3.0 - 7.5	1.09	24.8	50
3246	6.81 ± 0.18	3.5 - 11.0	1.29	18.9	50
MONTANA					
3248	5.00 ± 0.13	3.0 - 7.5	0.94	18.8	50
3250	5.92 ± 0.23	4.0 - 12.0	1.63	27.5	50
SOUTH DAKOTA					
3238	5.86 ± 0.19	4.0 - 10.0	1.37	19.9	50
WYOMING					
3134	5.79 ± 0.19	4.0 - 9.0	1.13	19.5	35
3252	8.10 ± 0.17	5.0 - 12.0	1.23	15.2	50
IDAHO					
2911	9.12 ± 0.70	4.0 - 16.0	4.92	54.1	50
2912	12.62 ± 0.80	8.0 - 19.0	5.68	21.8	50
3254	6.06 ± 0.09	4.0 - 9.5	0.66	10.9	50
3255	7.65 ± 0.07	5.5 - 12.0	0.49	6.4	50
NEBRASKA					
3224	9.78 ± 0.27	6.5 - 15.0	1.89	19.4	50
3231	5.65 ± 0.25	3.5 - 10.0	1.76	31.1	50
KANSAS					
3292	10.33 ± 0.32	6.5 - 15.5	2.23	22.5	50
COLORADO					
3153	9.61 ± 0.30	6.0 - 16.0	2.14	22.3	50
3261	9.73 ± 0.26	6.5 - 14.5	1.81	18.6	50
3262	8.03 ± 0.32	3.5 - 13.0	2.23	27.7	50
3263	9.59 ± 0.17	5.0 - 13.0	1.22	12.7	50
3264	7.36 ± 0.17	4.5 - 13.0	1.17	15.9	50
3265	8.62 ± 0.18	5.0 - 13.5	1.29	14.9	50
3161	9.02 ± 0.30	5.5 - 13.0	2.10	23.3	50
UTAH					
3150	10.56 ± 0.37	6.0 - 16.0	2.64	25.0	50
3151	11.20 ± 0.42	6.0 - 18.5	2.95	26.4	50
3256	10.38 ± 0.32	5.0 - 16.5	2.29	22.3	50
3258	5.39 ± 0.23	2.5 - 8.5	1.60	29.6	50
3259	5.61 ± 0.21	3.5 - 9.0	1.48	26.3	50
3136	4.98 ± 0.11	4.0 - 6.5	0.76	15.2	50
3141	9.59 ± 0.27	6.0 - 15.0	1.90	19.8	50
3142	9.85 ± 0.38	5.0 - 16.5	2.66	27.0	50
3143	10.75 ± 0.46	5.0 - 21.0	3.25	30.2	50
3145	7.77 ± 0.23	5.0 - 11.5	1.66	21.4	50
OREGON					
2905	9.26 ± 0.68	4.0 - 14.0	4.84	52.0	50
OKLAHOMA					
3289	12.12 ± 0.30	7.5 - 19.0	2.14	17.7	50
3290	8.91 ± 0.22	6.0 - 14.5	1.59	17.9	50
3291	15.31 ± 0.32	11.0 - 25.0	2.28	14.9	50
TEXAS					
3212	10.96 ± 0.43	6.0 - 15.5	3.04	27.8	50
3271	7.95 ± 0.29	5.5 - 17.0	2.03	25.5	50

3273	15.00 ± 0.53	8.5 - 22.0	3.78	25.2	50
3280	11.50 ± 0.32	8.0 - 16.0	2.24	19.5	50
3284	13.31 ± 0.21	7.5 - 19.0	1.50	11.3	50
3286	11.02 ± 0.51	6.5 - 21.0	3.58	32.4	50
3287	15.13 ± 0.54	9.0 - 23.0	3.82	25.3	50
3288	13.78 ± 0.39	8.0 - 19.0	2.73	19.8	50
NEW MEXICO					
3169	8.97 ± 0.31	4.5 - 14.5	2.22	24.8	50
3215	16.63 ± 0.49	10.0 - 28.5	3.45	20.7	50
3266	12.46 ± 0.25	5.5 - 17.5	1.77	14.2	50
3269	9.70 ± 0.30	5.0 - 15.0	2.15	22.2	50
ARIZONA					
2805	7.8 ± 0.45	4.0 - 11.0	3.18	40.7	50
2794	17.32 ± 1.15	10.0 - 28.0	8.14	33.2	50
2801	13.10 ± 0.81	6.0 - 19.0	5.74	62.7	50
CALIFORNIA					
2766	17.27 ± 1.37	10.0 - 27.0	9.70	56.1	50
2769	20.3 ± 1.26	13.0 - 29.0	7.48	36.8	35
2758	22.4 ± 1.97	10.0 - 38.0	13.90	62.1	50

ral conditions. This is according to expectations based on theoretical formulations and observations in other species.

There is a definite geographical correlation between plant height and latitude, the northern plants being generally smaller than the southern ones (fig. 4). This trend is slightly obscured by an east to west trend (western plants tend to be larger) of less magnitude and by the distributional relationship with the Rocky Mountains. *Gutierrezia sarothrae* is absent from higher elevations, but it grows in some of the valleys at lower elevations in the Rocky Mts. of Colorado, Wyoming, and Montana. The influence of altitude is not quite clear, but in any event plants north and east of the Rocky Mts. are smaller than those growing south and west. In the beginning I thought the differences found in plants of the two areas might merit subspecific recognition, but the present data do not warrant such a conclusion.

Tetraploid plants were found to be slightly larger than the average, but all populations fell well within the variation pattern of the diploids. Polyploid plants or populations cannot be distinguished from the diploids on the basis of plant height.

INVOLUCRE. The length and width of the involucre are related to the number and size of flowers in a head, and are presumably under the same selective control that affects the floral characteristics. The character has been measured in 50 plants in each of 41 different populations (table 3; fig. 5) the measurements having been made in the field with the aid of a caliper. Of all the characters studied, involucre dimen-

FIG. 5. Height and width of involucre; triangles drawn proportional to the mean values of the populations. Goode Base Map copyrighted by the University of Chicago.

sions, proved to be the least variable, notwithstanding the fact that the mean involucre length of the population with the longest involucre was twice that of the one with the shortest involucre (2.9-5.7 mm.) and the mean width of the widest involucres was 2.5 times the mean of the narrowest involucres (1.1-2.5 mm.). The shortest measured involucre was 2.2 mm., the longest 6.5 mm.; the narrowest was 0.9 mm., the widest 2.9 mm.; most involucres were between 3.0 mm. and 3.5 mm. long and 1.5-1.7 mm. wide. The coefficient of variation fluctuated around 10% with minimum and maximum values of 4.2 and 19.2%. There is a weak linear corre-

TABLE 3. MEAN, RANGE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR CHARACTERS OF THE INVOLUCRE

COLL. NO.	LENGTH				WIDTH			
	$\bar{x}$ ± st. er.	range	s	C(%)	$\bar{x}$ ± st. er.	range	s	C(%)
NORTH DAKOTA								
3243	3.95 ± .05	3.1 - 4.6	.38	9.7	1.61 ± .02	1.2 - 2.0	.14	8.8
3246	3.89 ± .05	3.2 - 4.9	.36	9.3	1.58 ± .02	1.3 - 2.1	.15	9.6
MONTANA								
3248	4.08 ± .06	3.2 - 5.0	.43	10.6	1.61 ± .02	1.3 - 1.9	.13	8.1
3250	3.97 ± .06	3.2 - 5.0	.42	10.6	1.58 ± .02	1.2 - 1.8	.17	10.5
SOUTH DAKOTA								
3238	3.57 ± .06	2.4 - 4.9	.46	12.8	1.52 ± .03	1.1 - 2.0	.18	12.0
WYOMING								
3252	4.15 ± .06	3.5 - 5.4	.41	9.8	1.61 ± .03	1.3 - 2.0	.18	11.5
IDAHO								
3254	3.80 ± .05	3.2 - 4.5	.37	9.7	1.60 ± .02	1.3 - 1.9	.14	8.6
3255	4.15 ± .03	3.4 - 4.6	.20	4.9	1.60 ± .02	1.3 - 1.8	.13	8.4
NEBRASKA								
3224	4.14 ± .08	3.1 - 5.8	.55	13.3	1.69 ± .05	1.2 - 2.9	.33	19.7
3231	4.25 ± .07	3.2 - 5.6	.48	11.3	1.70 ± .03	1.3 - 2.1	.20	11.5
KANSAS								
3292	4.01 ± .05	3.0 - 4.5	.37	9.3	1.57 ± .02	1.2 - 1.8	.15	9.2
COLORADO								
3261*	5.10 ± .06	4.3 - 6.2	.44	8.5	2.21 ± .03	1.8 - 2.7	.21	9.6
3262	3.98 ± .06	3.2 - 5.0	.41	10.2	1.56 ± .02	1.3 - 1.8	.14	8.7
3263	4.36 ± .06	3.9 - 5.3	.42	9.6	1.76 ± .02	1.4 - 2.2	.14	9.1
3264	3.94 ± .04	3.3 - 4.5	.32	8.0	1.58 ± .02	1.3 - 1.8	.14	9.1
3265	3.83 ± .04	3.1 - 4.5	.32	8.3	1.52 ± .02	1.2 - 1.8	.12	7.8
UTAH								
3150	3.85 ± .05	3.2 - 4.8	.34	8.9	1.88 ± .03	1.4 - 2.2	.20	10.5
3151	3.94 ± .03	3.5 - 4.3	.21	5.3	1.76 ± .03	1.2 - 2.1	.20	11.4
3256	4.21 ± .06	3.4 - 5.2	.41	9.8	1.62 ± .02	1.2 - 2.1	.18	10.9
3258	3.94 ± .03	3.3 - 4.5	.21	5.5	1.71 ± .02	1.4 - 2.1	.15	8.6
3259	4.33 ± .06	3.5 - 5.1	.40	9.1	1.74 ± .01	1.3 - 2.3	.07	4.2
OKLAHOMA								
3290	3.99 ± .05	3.2 - 4.7	.34	8.5	1.62 ± .01	1.4 - 1.8	.08	5.3
3291	3.98 ± .06	2.7 - 4.5	.43	10.7	1.60 ± .02	1.3 - 1.9	.14	8.8
TEXAS								
3212*	3.23 ± .03	2.8 - 4.0	.19	5.9	1.61 ± .03	1.2 - 2.0	.18	11.0
3271	3.16 ± .03	2.8 - 3.6	.22	6.9	1.32 ± .02	1.0 - 1.6	.13	10.0
3273*	3.12 ± .05	2.7 - 3.8	.35	11.4	1.37 ± .02	1.1 - 1.8	.16	11.3
3280	3.51 ± .04	2.9 - 4.2	.32	9.0	1.45 ± .02	1.2 - 1.7	.11	7.9
3284	3.82 ± .05	2.2 - 4.3	.38	9.9	1.55 ± .02	1.1 - 1.8	.13	8.6
3286	3.90 ± .04	3.3 - 4.5	.29	7.7	1.61 ± .02	1.3 - 1.9	.14	8.8
3287	4.02 ± .05	3.4 - 4.8	.39	9.6	1.63 ± .02	1.3 - 1.9	.13	8.2
3288	3.85 ± .04	3.3 - 4.4	.28	7.3	1.57 ± .02	1.4 - 1.8	.12	7.7
NEW MEXICO								
3169*	3.57 ± .02	3.1 - 4.0	.16	4.6	1.76 ± .02	1.2 - 2.1	.13	7.6
3215	3.72 ± .03	3.3 - 4.2	.23	6.2	1.67 ± .03	1.4 - 2.0	.18	10.6
3266	4.07 ± .05	3.3 - 4.9	.36	8.8	1.54 ± .02	1.3 - 1.7	.12	7.9
3269	2.93 ± .03	2.5 - 3.3	.24	8.2	1.14 ± .02	.9 - 1.5	.11	10.1
ARIZONA								
2794*	5.65 ± .12	4.5 - 6.5	.85	15.1	2.12 ± .04	1.8 - 2.8	.25	11.7
2801	3.73 ± .02	2.7 - 4.3	.16	4.3	1.96 ± .03	1.3 - 2.5	.23	11.9
2805	3.92 ± .04	3.5 - 4.9	.26	6.6	1.67 ± .04	1.1 - 2.7	.25	15.1
CALIFORNIA								
2766	3.51 ± .03	2.5 - 4.5	.24	6.7	1.85 ± .04	1.3 - 2.7	.27	14.5
2769	3.43 ± .08	2.7 - 3.9	.60	17.5	2.15 ± .06	1.5 - 2.5	.41	19.2
2758	4.36 ± .08	3.5 - 4.9	.56	15.1	2.48 ± .04	1.9 - 2.9	.27	11.7

*Polyploid populations (n = 8).

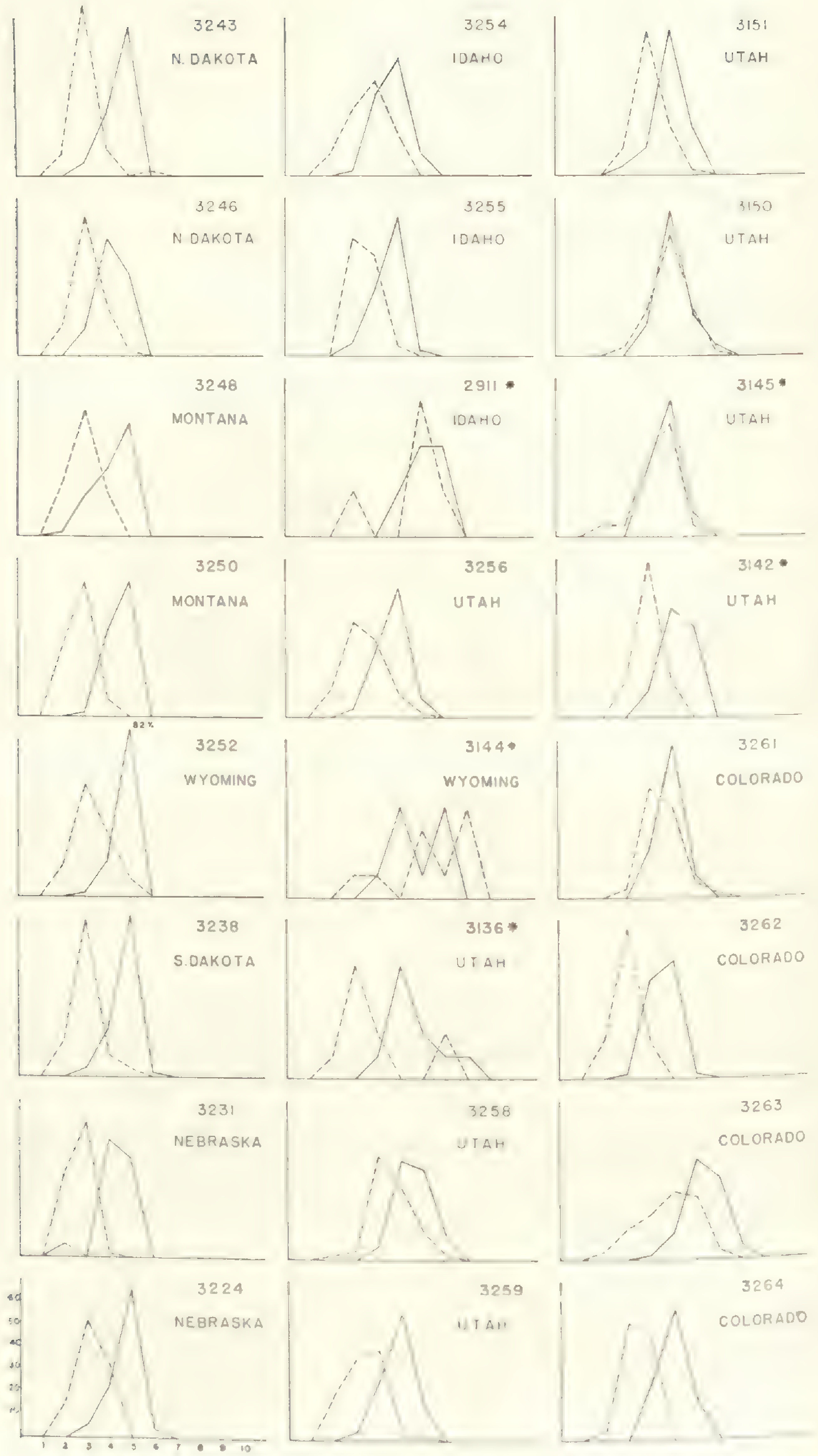

FIG. 6. Frequency distribution of tubular (dotted lines) and ligulate (full lines) flowers per head in populations of *G. sarothrae*. Asterisks indicate samples of less than 50 plants. For exact localities see appendix.

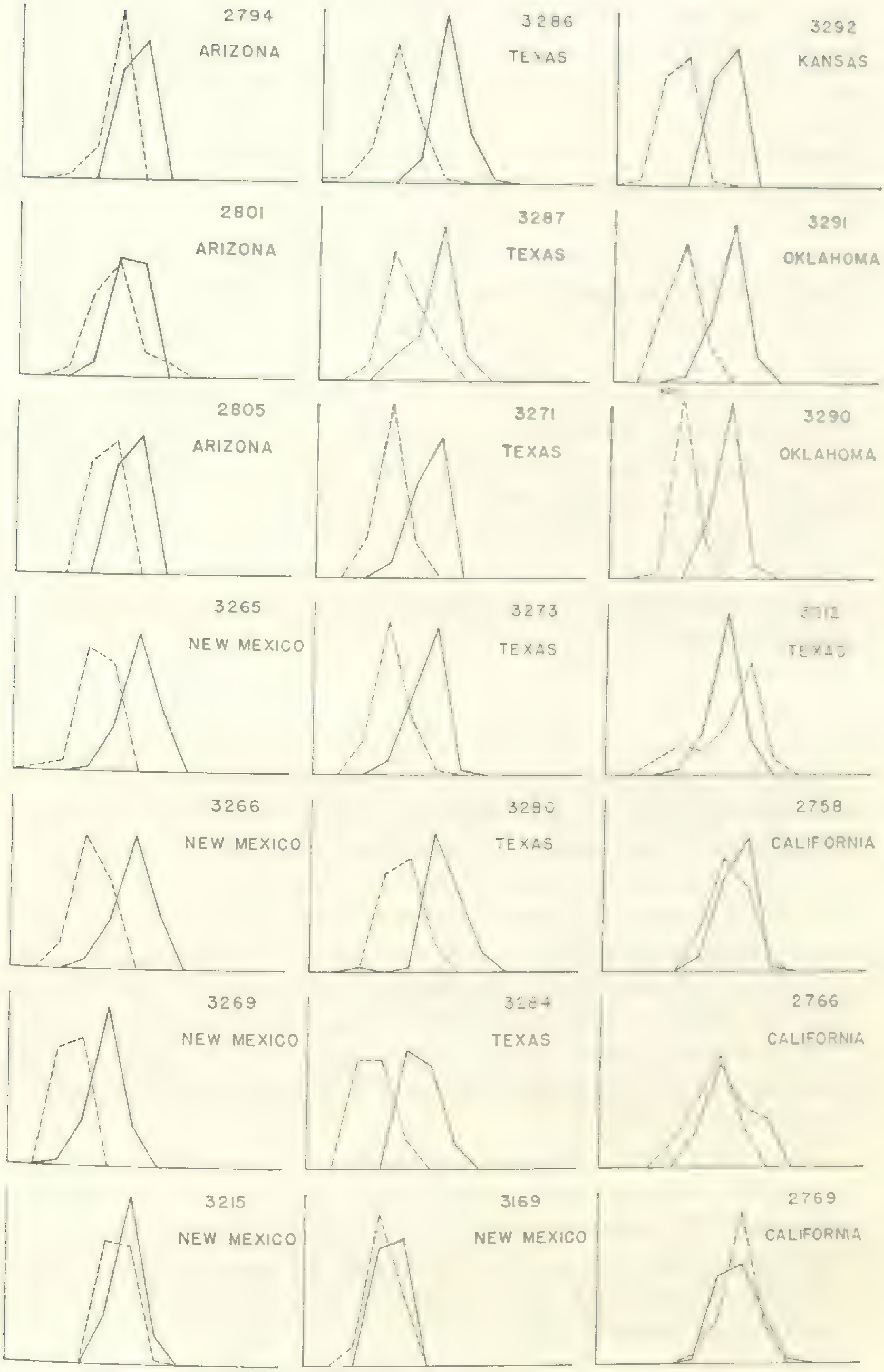

FIG. 7. Frequency distribution of tubular (dotted lines) and ligulate (full lines) flowers per head in popuations of *G. sarothrae*. For exact localities see appendix.

lation between length and width of the involucre, obscured in part by a large amount of scattering. No correlation could be observed between dimensions of the involucre and geographical distribution, aside from the slightly larger sized involucre of the California populations (table 3; fig. 6). Degree of variation was relatively uniform, the differences observed being randomly distributed.

Two polyploid populations (3261 and 2794) have significantly larger involucres than all the other populations measured; the other three polyploid populations have involucres slightly smaller than the average. Although it is possible that many of the plants with very large involucres that have been collected repeatedly are polyploids, no generalization that polyploids always have larger involucres can be made as far as *Gutierrezia sarothrae* is concerned.

The shape of the involucre in all cases, was the characteristic turbinate one of the species. No significant differences in this character were detected between any of the populations studied.

NUMBER OF FLOWERS. Of all the characteristics studied, number of flowers per head is the most interesting for several reasons: it was the main "key" character used to distinguish the many species erected within the complex; it shows the greatest amount of variability, at least among the characteristics investigated; it is potentially the feature most directly subjected to selection by pollinators; and it illustrates best some of the puzzling problems encountered in the morphological analysis.

There are two main components to consider: number of ligulate and number of tubular flowers in a head. These are not entirely independent of each other as we will see further on, but for the purpose of analysis they are best treated independently (table 4).

The number of ligulate flowers in a head ranges between 2 and 8, but over 50% of the heads counted had 5 ligulate flowers. The mean of 30 of the 41 populations analyzed was between 4 and 5; of the remaining 12 populations, 8 had values between 5.01 and 6.00, one had a mean of 6.32 and two had values below 4. The coefficient of variability was usually between 11 and 15%, with a low of 9.5% and a high of 26.7%. Since number of flowers is a discrete and not a continuous variable it is obvious that we only have seven

TABLE 4. MEAN, RANGE, MODE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR NUMBER OF FLOWERS IN A HEAD

POP. NO.	LIGULATE FLOWERS				TUBULAR FLOWERS			
	$\bar{x}$ ± *st. er.*	*range & mode*	*s*	*C (%)*	$\bar{x}$ ± *st. er.*	*range & mode*	*s*	*C (%)*
NORTH DAKOTA								
3243	4.60 ± .09	3 - 5 (5)	.61	13.2	3.08 ± .09	2 - 6 (3)	.64	20.8
3246	4.24 ± .09	3 - 5 (4)	.65	15.4	3.12 ± .09	2 - 5 (3)	.66	21.0
MONTANA								
3248	4.28 ± .12	2 - 5 (5)	.83	19.5	2.96 ± .10	2 - 4 (3)	.67	22.7
3250	4.58 ± .08	3 - 5 (5)	.54	11.7	2.76 ± .08	2 - 4 (3)	.59	21.4
SOUTH DAKOTA								
3238	4.72 ± .08	3 - 6 (5)	.57	12.1	3.02 ± .09	2 - 5 (3)	.66	21.7
WYOMING								
3252	4.80 ± .07	3 - 5 (5)	.46	9.5	3.30 ± .11	2 - 5 (3)	.81	24.4
IDAHO								
3254	4.70 ± .10	3 - 6 (5)	.67	14.3	3.74 ± .11	2 - 5 (4)	.77	20.6
3255	4.60 ± .09	3 - 6 (5)	.64	13.9	3.52 ± .08	3 - 5 (3)	.57	16.3
NEBRASKA								
3224	4.68 ± .09	3 - 6 (5)	.65	14.0	3.16 ± .10	2 - 4 (3)	.70	21.5
3231	4.36 ± .10	2 - 5 (4)	.70	16.1	2.64 ± .08	2 - 4 (3)	.54	20.4
KANSAS								
3292	4.56 ± .07	4 - 5 (5)	.50	10.9	2.54 ± .08	1 - 4 (3)	.57	22.5
COLORADO								
3261	4.88 ± .08	4 - 6 (5)	.56	11.4	4.54 ± .11	3 - 7 (4)	.76	16.8
3262	4.54 ± .08	3 - 6 (5)	.57	12.6	2.98 ± .08	2 - 4 (3)	.59	19.7
3263	6.32 ± .12	4 - 8 (6)	.85	13.4	4.76 ± .18	2 - 7 (5)	1.24	26.0
3264	4.90 ± .09	4 - 6 (5)	.64	13.0	3.40 ± .08	2 - 4 (3)	.57	16.9
3265	5.20 ± .10	3 - 6 (5)	.71	13.7	3.36 ± .10	1 - 4 (3)	.67	20.0
UTAH								
3150	5.12 ± .10	4 - 7 (5)	.69	13.5	4.96 ± .11	3 - 7 (5)	.81	16.3
3151	5.00 ± .10	3 - 6 (5)	.70	14.0	4.14 ± .09	3 - 6 (4)	.64	15.5
3256	4.70 ± .10	3 - 6 (5)	.67	14.3	3.48 ± .13	2 - 6 (3)	.88	25.4
3258	5.54 ± .11	4 - 7 (5)	.76	13.6	4.52 ± .13	2 - 7 (4)	.93	20.5
3259	4.80 ± .10	3 - 6 (5)	.73	15.2	3.30 ± .13	2 - 6 (4)	.88	26.8
OKLAHOMA								
3290	4.84 ± .07	4 - 6 (5)	.51	10.5	3.12 ± .07	2 - 4 (3)	.50	16.0
3291	4.82 ± .09	3 - 6 (5)	.62	12.9	2.84 ± .09	2 - 4 (3)	.64	22.5
TEXAS								
3212	4.92 ± .09	3 - 6 (5)	.60	12.2	5.06 ± .19	2 - 7 (6)	1.36	26.9
3271	4.50 ± .09	3 - 5 (5)	.61	13.5	2.98 ± .08	2 - 4 (3)	.56	18.7
3273	4.58 ± .09	3 - 6 (5)	.64	14.0	3.12 ± .09	2 - 5 (3)	.66	21.2
3280	5.40 ± .13	2 - 7 (5)	.91	16.8	3.68 ± .10	3 - 5 (4)	.71	19.4
3284	4.62 ± .10	4 - 6 (4)	.67	14.5	2.68 ± .10	2 - 4 (3)	.68	25.5
3286	5.14 ± .09	4 - 7 (5)	.62	12.1	3.04 ± .12	0 - 6 (3)	.86	28.1
3287	4.72 ± .11	3 - 6 (5)	.78	16.5	3.48 ± .11	2 - 5 (3)	.78	22.4
NEW MEXICO								
3169	3.52 ± .07	3 - 4 (4)	.51	14.4	3.22 ± .08	2 - 4 (3)	.58	17.9
3215	4.92 ± .08	4 - 6 (5)	.57	11.6	4.52 ± .08	4 - 6 (4)	.54	11.9
3266	4.94 ± .11	3 - 6 (5)	.77	15.6	3.26 ± .09	2 - 4 (3)	.64	19.6
3269	3.94 ± .09	2 - 5 (4)	.66	16.6	2.52 ± .07	2 - 3 (3)	.50	19.8
ARIZONA								
2794	4.60 ± .07	4 - 5 (5)	.50	10.9	3.60 ± .18	0 - 4 (4)	1.30	36.1
2801	4.40 ± .08	3 - 5 (4)	.60	13.7	3.80 ± .13	2 - 6 (4)	.90	23.7
2805	4.60 ± .07	4 - 5 (5)	.50	10.9	3.50 ± .07	3 - 4 (4)	.50	14.3
CALIFORNIA								
2766	5.50 ± .21	4 - 7 (5)	1.47	26.7	4.60 ± .15	0 - 6 (5)	1.09	23.6
2769	5.80 ± .12	4 - 8 (6)	.84	14.5	5.90 ± .10	4 - 7 (6)	.70	11.9
2758	5.50 ± .09	4 - 7 (6)	.65	11.8	5.30 ± .11	4 - 7 (5)	.77	14.5

classes altogether (2, 3, 4, 5, 6, 7, 8) and at first glance it appears that the differences observed between populations might be significant. Nevertheless three of the seven classes (2, 7, 8) are present only occasionally. In 32 populations the modal class was five, in six it was four and in three it was six. Only the populations with six and four could be considered as differing sufficiently to be of taxonomic importance. However, if we look at the frequency distributions of ligulate flowers in a head (figs. 6 and 7), we see that there is a considerable overlap between most populations. The possible explanation for the variation in mean and modal number between populations is discussed below (see under discussion of eco-geographic differentiation).

The picture revealed by the data on number of tubular flowers in a head is similar to that shown by the ligulate flowers, with minor variations. The modal class is three tubular flowers per head. This class characterizes only 24 out of 41 populations; four is the next most common, being the modal class in 11 populations; five is the most abundant class in four populations; and finally two populations have heads mostly with six tubular flowers. Individual heads with between none and seven tubular flowers have been found. It is clear that the number of tubular flowers per head is a more variable character than the number of ligulate flowers per head, and this is reflected by the coefficient of variation which fluctuates between 11.9% and 36.1%, with most populations having values around 20%.

If we examine the relation between ligulate and tubular flowers we can see that they are not independent of each other but are directly correlated. On the basis of the observed frequencies of the modal classes, the expected number of populations with a certain number of ligulate and tubular flowers was calculated and compared with the observed numbers (table 5). It will be noted that the classes with a similar number of ligulate and tubular flowers such as 4/3, 6/5, 5/3, 5/4, 6/5 and 6/6 are found in the expected numbers or in higher frequencies than expected, while in combinations such as 4/5, 4/6, 6/3 and 6/4 where the number of ligulate and tubular flowers is more unequal, the observed numbers (zero) are less than the percentage (10%) of the total expected (4). The correlation between ligulate and tubular flowers is shown graphically in fig. 8, where in addition to

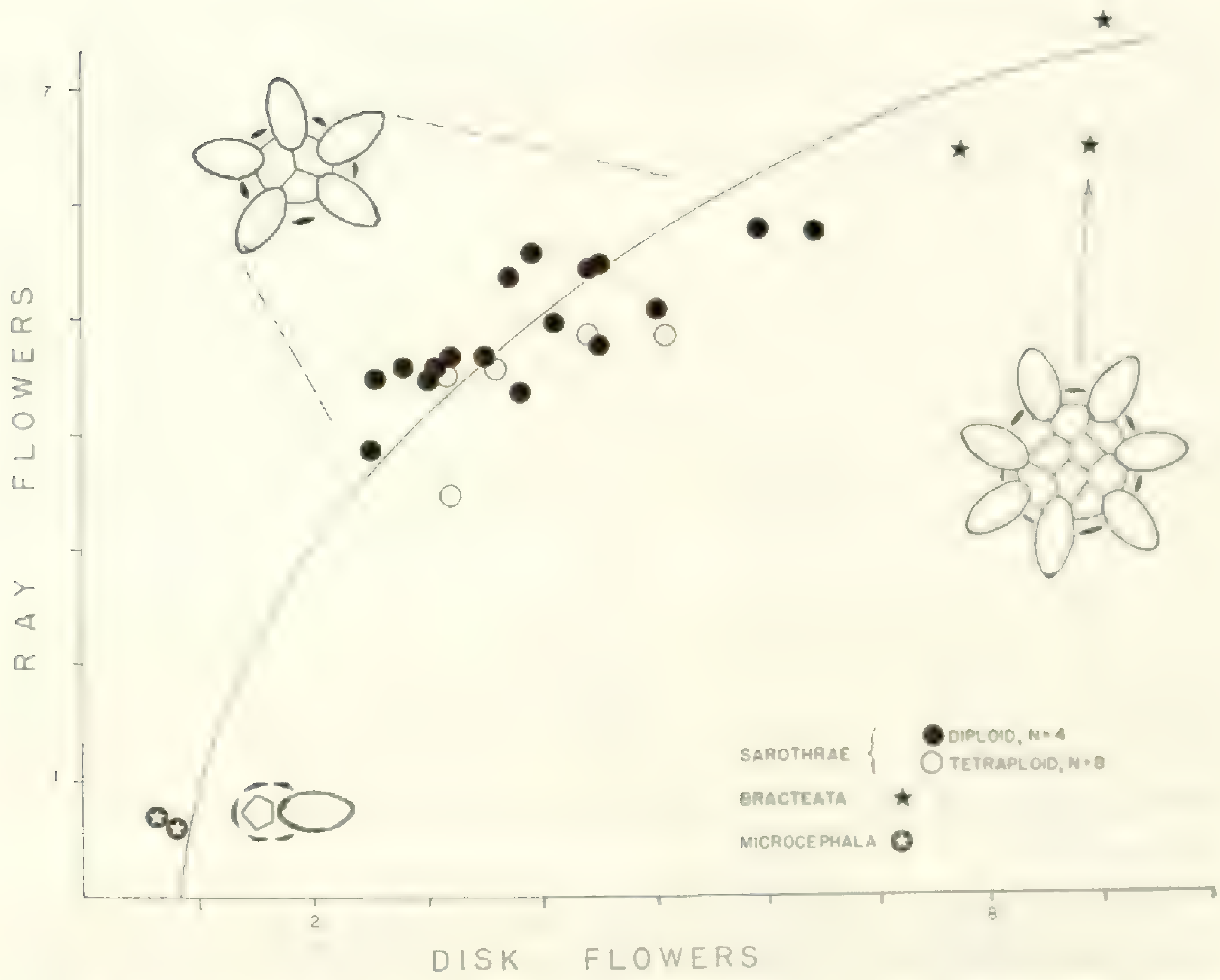

Fig. 8. Regression curve showing correlation between number of ligulate and tubular flowers in a head.

Gutierrezia sarothrae populations, data from other species have been plotted. The regression can be clearly seen, and it also can be observed that it is parabolic rather than linear. The reason for this is clear. Since in a capitulum of *Gutierrezia* there is only one row of ligulate flowers, as the total number of flowers in a head increases the ligulate flowers in the periphery increase in relation to the diameter of the head (a linear function), while the tubular flowers increase in relation to the surface of the head (a geometric function). Some latitude is of course present as in all biological material, and changes in relative size of the flowers or in the convexity of the receptacle, can affect this relationship to a certain extent. Finally, it should be pointed out that flowers at various stages of abortion were occasionally found. These were counted when discovered, but it is almost certain that some have been overlooked, introducing another source of error. It would be very interesting to investigate the morphogenetic processes involved in the formation of ligulate and tubular flowers where a better explanation of the corre-

TABLE 5. EXPECTED AND OBSERVED MODAL NUMBERS OF TUBULAR AND LIGULATE FLOWERS IN A HEAD

CLASSES		EXPECTED		OBSERVED	
Ligulate flowers	Tubular flowers	%	No. pop.	%	No. pop.
4	3	9	4	12.5	5
4	4	4	1	3	1
4	5	2	1	—	—
4	6	1	1	—	—
5	3	47	19	47.5	19
5	4	20	8	25	10
5	5	8	3	5	2
5	6	4	1	3	1
6	3	4	1	—	—
6	4	2	1	—	—
6	5	1	1	5	2
6	6	.4	—	3	1
		102.4	41	104	41

lation between these two types of flowers might be expected to be found.

There is some correlation between numbers of flowers and geographical distribution. All the populations north and east of Colorado are fairly uniform with mostly modal classes of 5 ligulate and 3 tubular flowers and mean values of approximately 4.50-4.80 for ligulate flowers and 2.80-3.10 for tubular flowers. The populations in Colorado and Utah are more variable, with a tendency to higher values for both ligulate and tubular flowers, and a similar situation is found in some Texas populations. Two populations in New Mexico had values of less than four for ligulate flowers; and, finally, the three California populations studied had consistently higher values than the average. The significance of these variations is hard to assess, but it is possibly related to the more optimal conditions of the populations nearer to the center of distribution than those towards the periphery (for further information see under discussion). No correlation could be detected between chromosome number and number of flowers in a head.

PAPPUS. The pappus in the flowers of *Gutierrezia sarothrae* is formed by 6 to 9 short paleaceous bracts. In this respect *Gutierrezia* is an exceptional genus in the tribe *Astereae* where the genera generally have a pappus formed by well developed bristles, or wanting by reduction. The pappus of *Gutierrezia* is of a type that is also characteristic

Table 6. Mean, Range, Standard Deviation and Coefficient of Variation for Pappus Lengths

COLL. NO.	TUBULAR FLOWERS				LIGULATE FLOWERS			
	x ± st. er.	*range*	*s*	*C(%)*	*x ± st. er.*	*range*	*s*	*C(%)*
NORTH DAKOTA								
3243	1.39 ± .03	1.0 - 1.9	.24	17.1	.59 ± .03	.3 - 1.1	.21	32.2
3246	1.48 ± .03	1.0 - 2.0	.18	17.3	.72 ± .02	.3 - 1.2	.21	29.2
MONTANA								
3248	1.36 ± .03	1.0 - 2.0	.25	18.2	.84 ± .03	.5 - 1.2	.18	21.6
3250	1.44 ± .03	1.0 - 2.0	.24	16.7	.71 ± .03	.3 - 1.2	.22	30.5
SOUTH DAKOTA								
3238	1.17 ± .03	.8 - 1.6	.23	19.8	.42 ± .01	.2 - .8	.10	23.4
WYOMING								
3252	1.26 ± .03	.8 - 1.8	.21	16.4	.53 ± .03	.2 - 1.2	.21	39.3
IDAHO								
3254	1.28 ± .02	1.0 - 1.7	.17	13.6	.63 ± .03	.3 - 1.0	.18	28.3
3255	1.34 ± .03	1.0 - 1.7	.19	14.5	.73 ± .02	.4 - 1.2	.16	22.5
NEBRASKA								
3224	1.34 ± .03	1.0 - 2.0	.23	17.1	.75 ± .03	.4 - 1.4	.22	29.0
3231	1.38 ± .04	1.0 - 2.0	.27	19.3	.60 ± .03	.3 - 1.0	.18	30.5
KANSAS								
3292	1.27 ± .02	1.0 - 1.7	.15	12.1	.59 ± .02	.4 - .8	.11	19.0
COLORADO								
3261	1.40 ± .03	1.1 - 2.0	.20	14.6	.69 ± .03	.4 - 1.2	.18	26.1
3262	1.24 ± .03	.9 - 1.8	.22	17.6	.60 ± .02	.3 - .9	.16	26.3
3263	1.22 ± .03	.8 - 1.8	.21	16.9	.50 ± .02	.2 - 1.0	.14	27.7
3264	1.36 ± .04	.8 - 1.8	.26	19.4	.58 ± .02	.3 - 1.0	.17	28.6
3265	1.22 ± .03	.8 - 1.8	.21	17.2	.52 ± .02	.2 - .8	.13	25.6
UTAH								
3150	1.05 ± .03	.6 - 1.5	.19	17.7	.52 ± .01	.3 - 1.1	.09	16.7
3151	1.54 ± .04	1.2 - 2.1	.30	19.5	.75 ± .03	.4 - 1.5	.21	28.1
3256	1.31 ± .02	1.1 - 1.7	.17	13.0	.71 ± .03	.3 - 1.2	.18	25.5
3258	1.28 ± .03	1.0 - 1.8	.20	15.5	.64 ± .02	.4 - .8	.11	17.3
3259	1.21 ± .03	.9 - 1.8	.19	15.4	.57 ± .02	.3 - .9	.16	28.2
OKLAHOMA								
3291	1.22 ± .02	.9 - 1.7	.16	13.0	.55 ± .02	.4 - .8	.12	20.9
TEXAS								
3212	1.19 ± .02	1.0 - 1.4	.14	11.4	.64 ± .02	.3 - .9	.13	20.9
3271	1.13 ± .02	.9 - 1.5	.16	14.4	.50 ± .01	.2 - .7	.09	18.9
3273	1.21 ± .02	1.0 - 1.7	.14	11.2	.64 ± .03	.3 - 1.2	.18	27.8
3280	1.19 ± .02	.9 - 1.5	.14	12.1	.44 ± .02	.3 - .8	.12	28.4
3284	1.22 ± .03	.6 - 1.7	.22	17.8	.52 ± .02	.2 - .8	.13	25.5
3286	1.20 ± .03	.9 - 1.6	.24	20.0	.59 ± .02	.3 - .8	.13	21.8
NEW MEXICO								
3169	1.11 ± .03	.6 - 1.5	.21	18.8	.59 ± .02	.4 - .9	.12	20.2
3215	1.10 ± .02	.9 - 1.5	.12	11.1	.59 ± .02	.3 - .9	.14	23.4
3266	1.30 ± .04	.9 - 1.9	.25	19.3	.56 ± .02	.3 - .9	.14	25.7
3269	1.25 ± .03	1.0 - 1.8	.18	14.6	.52 ± .02	.3 - .8	.15	29.5
ARIZONA								
2794	1.66 ± .02	1.2 - 2.0	.16	9.5	1.07 ± .02	.7 - 1.3	.12	10.9
2801	1.06 ± .02	.8 - 1.4	.14	13.0	.36 ± .01	.2 - .5	.07	18.6
2805	1.18 ± .01	1.0 - 1.5	.11	8.9	.52 ± .01	.3 - .9	.10	18.3
CALIFORNIA								
2766	1.14 ± .02	.8 - 1.5	.16	13.7	.59 ± .02	.2 - .9	.17	28.3
2769	.93 ± .01	.5 - 1.1	.10	11.2	.34 ± .01	.2 - .5	.08	22.4
2758	1.46 ± .02	1.2 - 1.9	.16	11.0	.58 ± .01	.4 - .8	.10	17.4

of a group of related genera including *Grindelia, Amphiachyris, Xanthocephalum* and *Olivaea.* This pappus type is more like that of many genera of *Heliantheae* than of the *Astereae* generally, and it can be considered to be a primitive character.

Measurements were made of the length of the pappus of the tubular and ligulate flowers. The pappus of the tubular flowers is roughly twice the length of the pappus of the ligulate flowers. The results are summarized in table 6.

The main function of the pappus is that of aiding in the dispersal of the fruit. The agent dispersing many of the *Compositae* fruits is the wind, and the bristly pappus of such genera of *Astereae* as *Erigeron, Conyza, Haplopappus* and *Aster* is particularly well adapted to dispersal by wind. The paleaceous pappus of the *Heliantheae* and *Gutierrezia* may be interpreted either as a transitional stage between the ancestral calyx and an advanced bristly pappus, or it may be considered as a particular adaptation to dispersal by agents other than wind, especially animals. More experimental evidence is needed to clarify this point and phylogenetic considerations should be brought to bear on the problem. In any event, in *Gutierrezia* the structure is somewhat reduced and no obvious function has been discovered. In view of this, it is of interest to see the amount of variation present in this structure.

The length of the pappus is remarkably uniform from population to population, the mean varying from 0.93 mm. to 1.48 mm. for the tubular flowers and from 0.34 mm. to 1.07 mm. for the ligulate flowers. The coefficient of variation varies from 9.5% to 20% for the pappus of the tubular flowers and from 10.9% to 32.2% for the pappus of the ligulate flowers. The greater variability in the pappus of the ligulate flowers is of interest. Part of the variation is due to experimental error, which in such a small structure becomes an important element, but not all of the higher variability of this structure compared to that of the tubular flowers can be ascribed to experimental error alone. The pappus of the ligulate flowers is very reduced, and in all likelihood no longer functional. The variability could be due to a relaxation of selection pressure for whatever function it had, but I believe that this is not the likely explanation.

In this character we can observe a slightly larger interdeme variability towards the center of the range, than that observed towards the periphery.

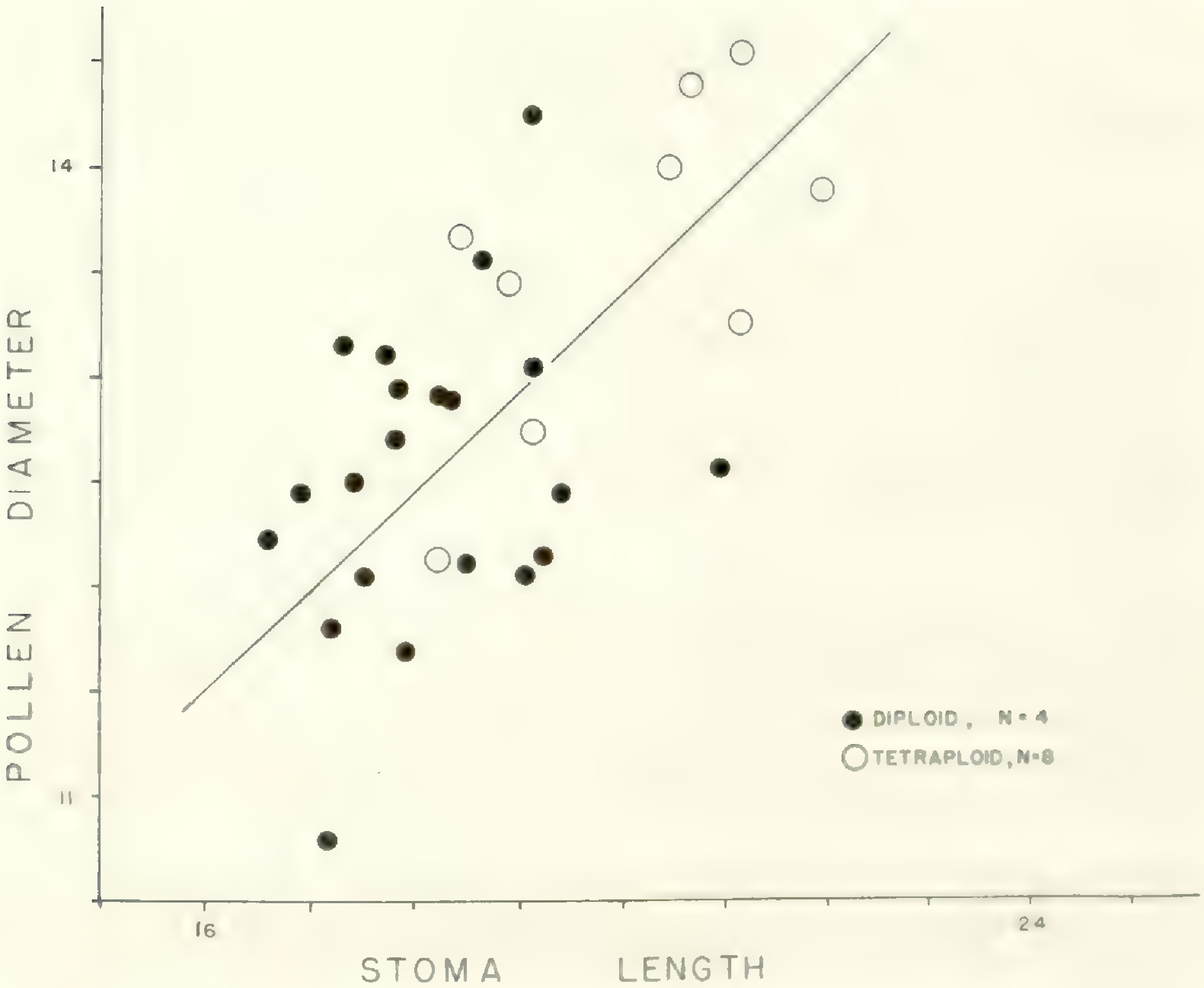

FIG. 9. Regression line between pollen diameter and stoma length.

POLLEN AND STOMATA. Pollen diameter is a cellular character. Also stoma length, being directly correlated with the size of the guard cells, is essentially a product of cell size. In general, in artificial tetraploids both pollen and stomata show an increase in size over the corresponding diploids. Comparative measurements of the structures are considered to be reliable sources of information for detecting polyploidy in herbarium specimens (Celarier and Mehra, 1958). The aim in measuring these characters was to see whether differences between the diploid and tetraploid populations were present.

The measurement of pollen grains and stomata was conducted entirely in the laboratory. Herbarium specimens of 32 populations for which chromosome counts were available were selected and 200 pollen grains and 50 stoma were measured from each plant. The results are summarized in table 7. There is an appreciable amount of variability in each sample especially in pollen size, considering it comes from a single plant. Although the polyploids tend to have larger dimensions (table 10; see also discussion under sibling and incipient species), there is a considerable amount of overlap.

TABLE 7. MEAN, RANGE, STANDARD DEVIATION AND COEFFICIENT OF VARIATION FOR POLLEN DIAMETER AND STOMA LENGTH

POP. NO.	POLLEN				STOMA			
	$\bar{x} \pm$ *st. er.*	*range*	*s*	*C*	$\bar{x} \pm$ *st. er.*	*range*	*s*	*C*
NORTH DAKOTA								
3245	12.9 ± .15	11 - 15	2.16	16.7	18.4 ± .3	16 - 22	2.38	12.9
MONTANA								
3249	12.1 ± .05	11 - 13	.76	6.3	19.2 ± .3	15 - 23	1.77	9.2
3250	12.3 ± .05	11 - 14	.64	5.2				
SOUTH DAKOTA								
3233*	14.4 ± .08	12 - 17	1.10	7.7	20.7 ± .2	18 - 24	1.73	8.4
3236	13.1 ± .02	12 - 15	.27	2.1	19.1 ± .2	17 - 21	1.09	5.7
WYOMING								
3134	12.5 ± .07	10 - 14	1.06	8.5	17.4 ± .2	15 - 20	1.28	7.4
NEBRASKA								
3224	12.6 ± .05	11 - 14	.77	6.1	20.9 ± .2	17 - 24	1.50	7.2
3228	12.9 ± .03	12 - 15	.39	3.0	18.8 ± .2	15 - 23	1.73	9.2
KANSAS								
3292	12.4 ± .08	11 - 14	1.20	9.7	19.4 ± .2	15 - 22	1.25	6.4
COLORADO								
3261*	14.7 ± .06	13 - 16	.83	5.6	20.9 ± .3	18 - 24	2.14	10.2
3262	12.1 ± .05	11 - 13	.69	5.7	19.0 ± .2	16 - 22	1.26	6.6
UTAH								
3136	10.8 ± .05	9 - 13	.72	6.7	17.2 ± .1	15 - 20	1.05	6.1
3145	13.0 ± .05	12 - 15	.64	4.9	17.3 ± .2	15 - 20	1.42	8.2
3150	11.7 ± .03	10 - 15	.37	3.2	18.0 ± .2	16 - 20	1.15	6.4
3151					17.0 ± .2	15 - 20	1.23	7.2
3258	14.2 ± .06	13 - 16	.78	5.5	19.2 ± .2	17 - 22	1.45	7.6
3260	12.7 ± .07	11 - 14	1.03	8.1	17.8 ± .2	16 - 20	1.15	6.5
OKLAHOMA								
3289	12.9 ± .05	12 - 15	.68	5.3	17.8 ± .2	16 - 20	1.14	6.4
3290	13.5 ± .04	13 - 15	.52	3.9	18.6 ± .2	16 - 21	1.21	6.5
TEXAS								
3212*	13.4 ± .07	11 - 16	.93	6.9	18.9 ± .3	16 - 21	2.05	10.8
3271	12.1 ± .05	11 - 13	.67	5.5	17.5 ± .2	15 - 20	1.11	6.3
3273*	13.7 ± .05	13 - 16	.72	5.3	18.4 ± .2	15 - 21	1.18	6.4
3280	11.8 ± .05	11 - 13	.74	6.3	17.2 ± .1	15 - 19	1.04	6.0
3282*	12.2 ± .04	11 - 14	.55	4.5	18.2 ± .1	17 - 20	1.02	5.6
3283	12.2 ± .05	11 - 13	.71	5.8	16.6 ± .3	14 - 19	2.25	13.6
3286	13.2 ± .05	12 - 15	.64	4.8	17.7 ± .2	15 - 20	1.08	6.1
3287	12.1 ± .05	11 - 14	.72	6.0	18.3 ± .2	16 - 21	1.34	7.3
NEW MEXICO								
3169*	13.9 ± .09	11 - 17	1.23	8.8	21.9 ± .2	19 - 25	1.52	6.9
3269	12.5 ± .06	11 - 14	.86	6.9	16.9 ± .2	15 - 21	1.25	7.4
3270	13.2 ± .11	12 - 14	1.57	11.9				
ARIZONA								
2792*	14.0 ± .07	12 - 15	1.01	7.2	20.4 ± .2	18 - 23	1.67	8.2
2793*	12.9 ± .15	12 - 15	2.07	16.0	19.2 ± .2	16 - 21	1.08	5.6
2794*	13.3 ± .06	12 - 15	.86	6.4	21.1 ± .2	18 - 24	1.45	6.9
2802*					19.8 ± .2	17 - 23	1.24	6.3

*Plants polyploid (n = 8)

The low values for the coefficient of variation are due to the fact that the samples are from a single plant. No geographical pattern could be detected in the size variation of these two characters.

Flowering Period

When grown under uniform conditions in Berkeley, plants from different localities were observed to flower at different times (Solbrig, 1960). Similar observations were made again with plants grown at Cambridge. There is a gradient with plants from northern localities flowering earlier and usually being through the flowering period earlier than plants from farther south. For example, plants from Sheridan, Wyoming (3252) started blooming in Cambridge May 15; those of Dubois, Idaho (3254), a locality some 300 miles west but from about the same latitude, started blooming May 22, a week later; on the other hand the first date for the population from south of Pocatello, Idaho (3255), some 120 miles south from the previous populations, was June 10, about two weeks later than the second, and almost a month later than the first.

A record was made of the dates on which flowering material of *Gutierrezia sarothrae* has been collected, on the basis of herbarium specimens. The results are shown graphically in fig. 10. The investigation shows that there is no appreciable difference in first flowering dates but a definite trend for plants from northern localities to finish earlier was found. It is not too surprising to find this cline, which can almost be expected on the basis of the climatological

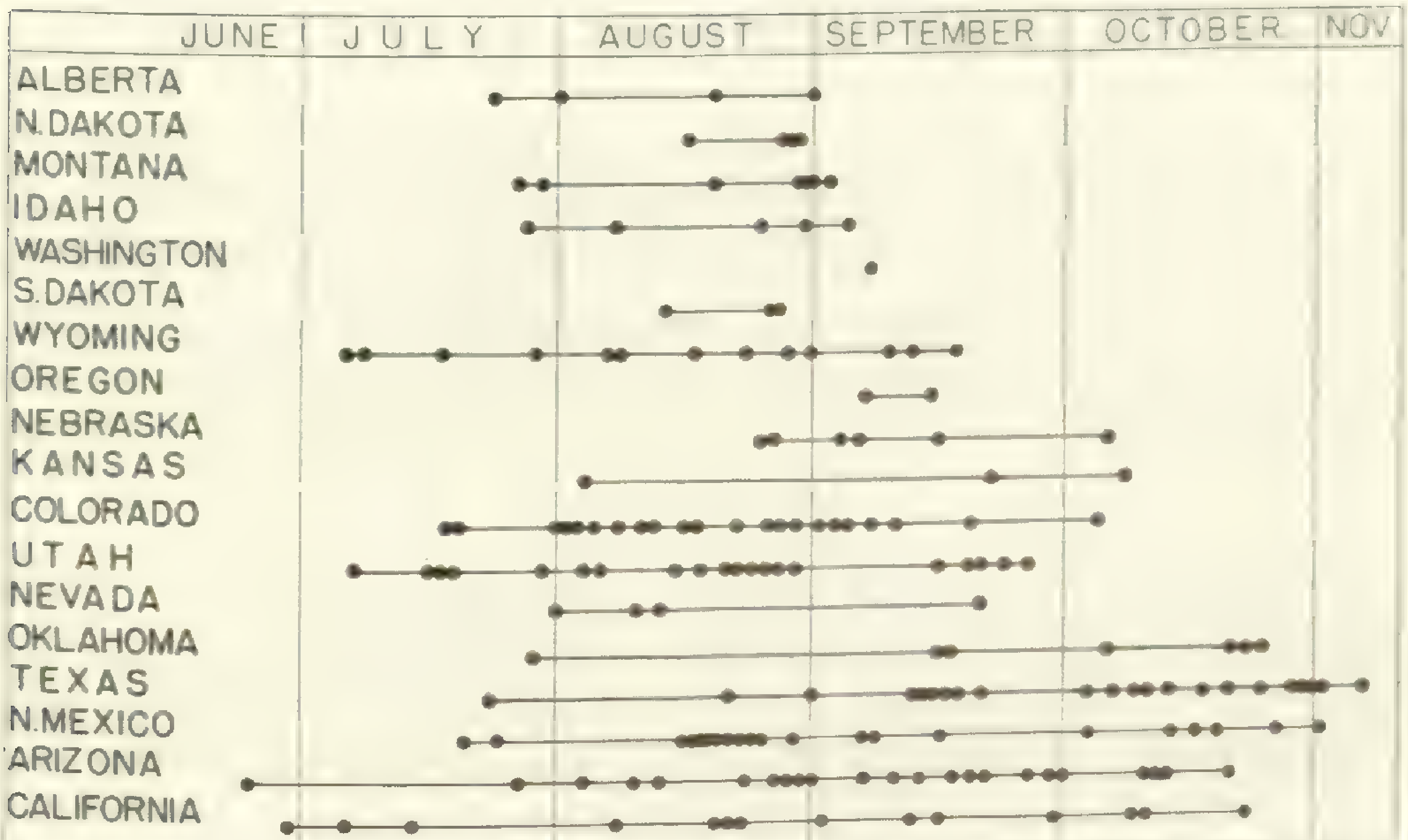

FIG. 10. Dates of blooming of populations of *G. sarothrae*. For further details see text.

factors of the environment (see under discussion). The earlier frosts in the northern area, and the shorter frost free period, diminish the growing season considerably, while the usually earlier summer rains in the more boreal areas apparently speed up the growth cycle. The earlier flowering dates of these plants under uniform conditions in culture as compared to the field are probably due to a faster rate of growth under the good conditions of the greenhouse or experimental field. The earliest date of blooming of wild populations throughout the range is most likely dependent on the date of the summer rains, a factor which fluctuates somewhat every year. Comparisons would be more meaningful if they were restricted to plants collected in the same year, which is not the case with the data of fig. 10. Field observations during the summer of 1961, made it very clear that there was this cline. Plants in North Dakota and Montana were in full bloom and forming seed at the end of August, while populations from Texas were just beginning to bloom in middle September.

The variation in plant size observed, and also the increase in stature of the plants from north to south, is most likely another expression of the shorter growing season, and an adaptation to these conditions.

POLLINATION[3]

In a previous paper concerning the North American species of *Gutierrezia* (Solbrig, 1960) I put forward the idea that new populations of *Gutierrezia* are probably initiated by a few seeds blown in from surrounding populations and that under favorable conditions the population might expand from these few pioneers to a few hundred plants. In such a situation the genotypes of the first members of the colony will be determined strictly by chance from the genotypes present in the neighboring populations. The probability of a certain genotype being selected is in direct proportion of its frequency in the area and the distance to the new available site. This is part of the process known as random

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[3] I want to express my appreciation for the help received from Drs. P. D. Hurd, Jr., E. G. Linsley, J. W. McSwain and R. H. Painter, in acquainting me with the literature and some of the problems of pollinators as viewed by entomologists. I also want to thank especially W. H. Anderson, K. V. Krombein, E. G. Linsley, C. F. W. Muesbeck, R. H. Painter, C. Sabrosky, T. J. Spilman and P. H. Timberlake for identifying my collections of insects.

genetic drift (Wright 1949; Dobzhansky, 1953), also known by the better designation of "founder principle" (Mayr, 1942). Another postulate was that a combination of the founder principle and selection by oligolectic bees could explain the uniformity within populations of *Gutierrezia*, and the differences between populations, assuming that no drastic differences existed in the selection pressures between different populations.

In order to test the role of pollinators in this scheme collections and observations of insects were made in a few different localities scattered throughout the range of *G. sarothrae*. The list of the particular pollinators collected is shown in table 8. A series of Diptera, Hymenoptera and Coleoptera are involved. In addition table 9 shows a few additional records taken from the literature. Of the major groups of pollinators only the Lepidoptera are absent. Observations were made at different times of day, and only insects observed visiting the heads of *Gutierrezia sarothrae* in medium to large numbers and feeding on pollen or nectar were collected, it was hoped that in this way occasional random visitors would not be picked up.

TABLE 8. POLLINATING INSECTS COLLECTED ON G. SAROTHRAE POPULATIONS, 1961

Pop. 3244. 7 mi. south of Dickinson, North Dakota. Aug. 27, 10 AM. *Anastoechus barbatus* O.S.; *Peleteria* aff. *clara* Curran; undet. *Meloideae.*

Pop. 3245. 12 mi. north of Belfield, North Dakota. Aug. 28, 10:30 AM. *Peleteria clara* Curran; *Poecilanthrax alpha* (O.S.); *P. willistonii* (Coq.); *Anastoechus barbatus* O.S.; *Cylindromyia californica* (Big.); *Villa flavocostalis* Painter; *Epicauta pennsylvanica* (De Geer).

Pop. 3246. Bridge over Little Missouri river and Hwy. 22, North Dakota. Aug. 28, 2 PM. *Anastoechus barbatus* O.S.; *Colletes* sp.; *Villa flavocostalis* Painter.

Pop. 3248. 2 mi. S. of Glendive on Hwy. 10, Montana. Aug. 29, 1 PM. *Poecilanthrax alpha* (O.S.); *Villa flavocostalis* Painter.

Pop. 3251. 5 mi. S. of Custer, Montana. Aug. 30, 10 AM. *Melissodes* sp.; *Colletes* sp.; *Poecilanthrax willistonii* (Coq.); *Peleteria malleola* (Big.); *Paradidyma singularis* (Tns.); *Chelonus sericeus* (Say); *Stenodynerus apache* Boh.

Pop. 3265. 5 mi. south of Trinidad, Colorado. Sept. 8, 12 noon. *Epicauta* sp.; *Chauliognatus lewisii* Croth.

Pop. 3269. 20 mi. north of Roswell on Hwy. 285, New Mexico. Sept. 10, 12 noon. *Calliopsis coloratipes* Ckll.; *Eucercis* sp.; *Exomalopsis solanii* Ckll.; *Melissodes* sp.; *Chauliognathus lewisii* Croth.

At the time of flowering of *Gutierrezia sarothrae,* late summer and fall, that is from about August to late October or early November, depending upon the latitude blooming ordinarily begins first and finishes earlier in the northern areas, there are not many other plants in bloom in the scrubland, juniper-piñon pine association, or semi-desert areas where *G. sarothrae* is found. The other plants in bloom at the time are for the most part yellow-flowered shrubby Compositae very similar in their inflorescence characters to *G. sarothrae.* Common genera in bloom at the time are *Chrysothamnus, Haplopappus, Grindelia, Tetradymia, Solidago,* and others.

The pollinating insects fall into two broad categories. The first group is the more abundant and is the group to which the bees (Hymnoptera) and bee-flies (Diptera-bombilids) belong. The behavior of these insects while they feed is to alight on a head inserting their tongues into one or several flowers and then to fly to another head, usually of another plant, where they repeat the process. They seem to be effective pollinators and are mostly involved in cross-pollination. They inflict no visible damage to the flowers.

The second group is that of the Coleoptera, particularly such genera as *Epicauta, Chauliognatus* and *Crossidius.* These insects feed on pollen, but instead of flying from flower to flower, they tend to crawl all over the plants, concentrating sometimes in large numbers (particularly *Epicauta*). They

TABLE 9. INSECTS REPORTED FEEDING ON FLOWERS OF G. SAROTHRAE[4]

Colletes laticinctus Timberlake; *C. intermixtus* Swenk; *C. phaceliae* Cockerell; *Heriades variolosa variolosa* (Cresson); *Crossidius wickhami* Casey; *C. jocosus* (Horn); *C. allgewahri* Le Conte; *Poecilanthrax sackenii sackenii* (Coq.); *Melissodes sabinensis nubila* LaBerge; *M. tepida* Cresson; *M. tepida timberlakei* Cockerell; *M. tesellata* LaBerge;

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[4] Data taken from the following works: Hurd, P. D. Jr. and C. D. Michener, "The Megachiline Bees of California (Hymenoptera: Megachilidae)", Bull. Calif. Insect Survey **3**: 1-247. 1955; La Berge, W. E. "A Revision of the Bees of the Genus Melissodes in North and Central America (Hymenoptera, Apidae)" Parts I-III, Univ. of Kansas Science Bull. **38-42**: 1956-61; Linsley, E. G. "Host Relationships in the genus Crossidius". Jour. Kansas Ent. Soc. **30**: 83-89. 1957. Painter, R. H. and J. C. Hall, "A monograph of the Genus Poecilanthrax (Diptera: Bombyliidae)" Kansas Agric. Exp. Station, Tech. Bull. **106**: 1-132, 1960; Stephen, W. P. "A Revision of the Bee Genus Colletes in America North of Mexico (Hymenoptera, Colletidae)" Univ. Kansas Science Bull. **36**: 149-527. 1954; Timberlake, P. H. "A Revisional Study of the bees of the genus Perdita F. Smith, with special reference to the fauna of the Pacific Coast (Hymenoptera, Apoidea)", Parts I-V. Univ. Calif. Publ. Ent., 1954-62.

M. plumosa LaBerge; *M. lustra* LaBerge; *M. stearnsi* Cockerell; *M. agilis* Cresson; *M. perlusa* Cockerell; *M. menuachus* Cresson; *M. semilupina* Cockerell; *M. bimatris* LaBerge; *M. fasciatella* LaBerge; *M. coreopsis* Robertson; *M. montana* Cresson; *M. tristis* Cockerell; *M. robustior* Cockerell; *M. hurdii* LaBerge; *M. pallidisignata* Cockerell; *M. subagilis* Cockerell; *M. limbus* LaBerge; *M. verbesinarum* Cockerell; *M. lutulenta* LaBerge; *M. utahensis* LaBerge; *M. brevipyga* LaBerge; *M. velutina* (Cockerell); *M. appressa* LaBerge; *M. microsticta* Cockerell; *M. paulula* LaBerge; *M. melanura* (Cockerell); *M. personatella* Cockerell; *M. sabinensis nubila* LaBerge; *M. tessellata* LaBerge; *Perdita semicrocea* Cockerell; *P. austini* Cockerell; *P. stottleri stottleri* Cockerell; *P. s. flavida* Swenk & Cockerell; *P. ericameriae* Timberlake; *P. oregonensis* Timberlake; *P. parilis* Timberlake; *P. luteola* Cockerell; *P. rhodura* Cockerell; *P. gutierreziae* Cockerell; *P. melastoma* Swenk & Cockerell; *P. rectangulata* Cockerell; *P. phymatae* Cockerell; *P. apacheorum* Timberlake.

are most effective in performing self-pollination (since they tend to carry pollen from one head to another in the same plant). In addition, they also do some damage to the flowers since on occasion they seem to feed on petals, styles, and anthers as well as pollen.

In addition to the insects mentioned, flowers of *Gutierrezia sarothrae* are also visited by parasitic wasps, apparently in the hope of ambushing their victims; diptera which parasitize the ovaries of *G. sarothrae;* and many other kinds of insects use the capitula as mating places. Not much if any pollination is effected by these visitors.

Although some species (such as members of the genus *Crossidius*) are larval parasites of roots of *Gutierrezia* and therefore spend their entire life cycle in association with this species, such a close relationship appears to be rare. Also, it has been reported that some of the bees *(Perdita)* are oligolectic to *Gutierrezia* in their feeding habits. This seems to be an exception, also. As a rule, a spectrum of various diptera, hymenoptera, and coleoptera feed as adults on *Gutierrezia* and other plants in bloom at the time. They rely on what plants are available, and, according to the literature, *Gutierrezia* is not considered to be a delicacy by insects, other plants apparently being preferred over it. None of the pollinators collected had exactly the same geographical distribution as *G. sarothrae*, although some, such as *Poecilanthrax willistonii*, come quite close (Painter & Hall, 1960).

Given the particular dispersed pattern of *Gutierrezia* where dense populations are often separated by considerable distances from each other, it is fairly safe to say that the amount of pollen carried from one population to the next is small, and probably is at zero or nearly so when the distance between populations is more than a mile. This situation with respect to the pollinating insects to a certain degree reinforces the isolation between populations, while the non-specificity both of the plant to the pollinators and vice-versa, to a certain extent assures pollination for the plant when it invades a new area.

In summary, *Gutierrezia* does not require a specific pollinator, pollination being effected by many different insects. The lack of dependence on a particular insect is due probably to the advantage of the species, particularly when it invades new areas. Furthermore, pollinators tend to reinforce the physical isolation of populations, but effect a fairly active transport of pollen within the population. This is facilitated, no doubt, by the almost universal dense aggregation of individual plants in populations of *G. sarothrae*. Exchange of genes between populations is, therefore, mostly restricted to seed dispersal. Finally, the thesis that insect pollinators might reinforce differences between populations by selecting a particular phenotype is not tenable, because of the large and diverse number of pollinators.

ENVIRONMENTAL FACTORS

A very important element in the diversity of morphological forms encountered in *G. sarothrae* is the wide range of environmental factors found over the area in which this species grows. The nature of this study did not permit a detailed study of the microenvironment, but the broad features of the environment are illuminating by themselves.

Temperature varies over the range of *G. sarothrae* between an annual mean of 40° F to about 70° F. The mean temperatures in the months of May through September fluctuate from 40° to 70° F in North Dakota, and from 60° to 80° F in Texas. July average minimum temperatures are between 40° and 70° in the whole zone from North Dakota to Texas, and July average maximum ranges between 70° and 100° F. Normal summer temperatures above 68° are present in North Dakota only between July 1 and August 15; in Utah from the middle of June to the end of August; in California from the middle of May to the middle of Novem-

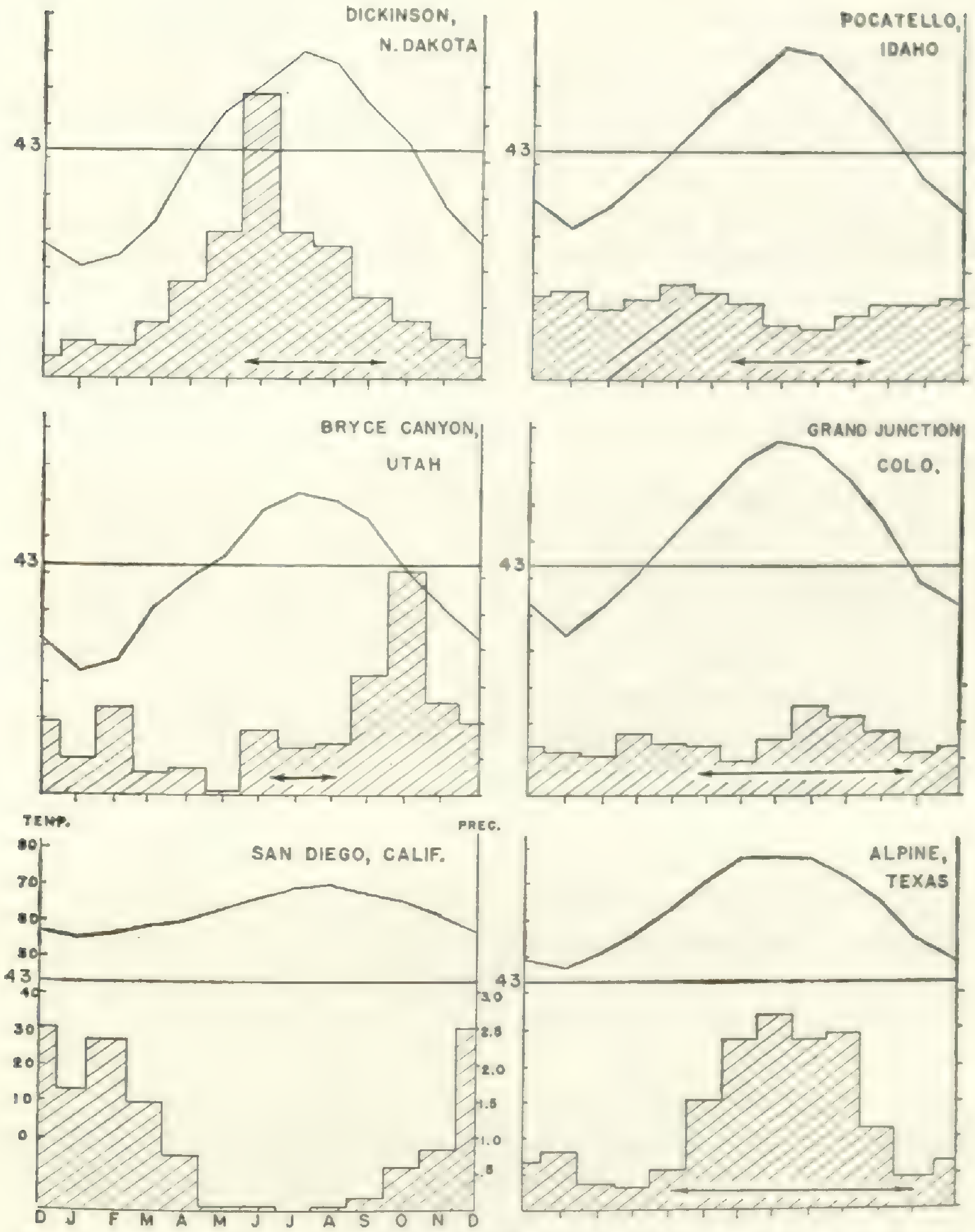


FIG. 11. Main climatological data of six sites sustaining populations of *G. sarothrae* in the immediate vicinity. Curve = mean temperature; hatched area = mean rainfall; arrow = frost free period. Area above 43° line is period of rapid growth. Data taken from the U. S. Weather Bureau.

ber. The rapid growing season (mean temperature above 43° F) in North Dakota starts in May and lasts through September; in Utah it starts in March and lasts through the middle of November; in California, Arizona and Texas temperatures above 43° F last throughout the year. The number of frost free days varies also quite drastically ranging from only about 100 days in Montana to about 300 in California.

The region where *G. sarothrae* grows has on the average an annual rainfall of not more than 20 inches but not less than 8 inches. Average July air humidity is less than 40% (noon and 8 PM data) in all the area but California where it is 60-70%. Monthly average figures for evaporation during the growing months of May through September vary from 5 to 12 inches; total normal average evaporation from May through October is 35-70 inches (in pans). The ratio of precipitation to evaporation for the normal frost free season varies from 0 to 20%; 90% or more of the years for which records are available had less precipitation than evaporation.

Another variable is day length. The longest day in June where the North Dakota populations grow is 16 hours; the longest day in June for the Texas populations is 14 hours; the shortest winter day in Texas is 10½ hours, in North Dakota 8 hours, 20 minutes. It is evident that a marked change occurs from north to south.

To summarize, *G. sarothrae* grows largely in an area with short, warm but not hot summers and cold winters (Montana, Idaho, North and South Dakota, Wyoming, Utah, W. Colorado, N. E. Arizona and N. W. New Mexico); in this area it is widespread but not too abundant, particularly in the more northerly parts. In also grows in areas with hot summers and cold winters (Arizona, New Mexico, Nebraska, Kansas and northern Oklahoma) and in areas with hot summers and mild winters (California, Texas and southern Oklahoma). The latter areas are less extensive than the first, but in them the species is in general more abundant. Where *G. sarothrae* grows it is very dry, as measured by air humidity, precipitation, and the precipitation/evaporation ratio. There is also a very marked gradient from north to south in length of the growing season, frost free days and length of day.

The terrain where the plant is found varies, but in general it does not grow at elevations above 2,000 m. The soil is loose, rocky, gravelly or sandy, with a high pH (7-9), and a low concentration of nitrates (Solbrig, 1960).

No precise data on microenvironmental factors are available, but observations show that the plants tend to favor areas of slightly higher moisture (protected slopes, flood beds, depressions, etc.) than adjacent sites, and also where soils are disturbed (soil slides, erosion gullies, etc.).

No precise pattern emerges from these data aside from the generalities already enunciated. But one is impressed by the great amount of variability and by the extremes of environment the species is capable of withstanding. Although there is not too much obvious direct correlation between the morphological variation and the environmental conditions indicated, there is a parallelism in the enormous amount of variation of both aspects that is worth noting.

DISCUSSION

VARIATION AND ECO-GEOGRAPHIC DIFFERENTIATION

From the foregoing presentation it is clear that we are dealing with a very variable group of plants. The variation can best be considered as that within and that between populations. An understanding of interpopulation variability is important for a better taxonomy. Speculation on the past history of the group, the general model of evolution of the complex, and how general or special a case is represented by *G. sarothrae* are all items of considerable interest.

Gutierrezia is not unique, neither in its wide tolerances nor in its high degree of plasticity. Many, if not most, plants have these characteristics to a greater or lesser degree. Transplant studies have shown that populations of such species vary in their specific tolerances to environmental factors and also in their morphology, and that these different responses are genetically fixed (Clausen, Keck & Hiesey, 1940; Böcher, 1963, etc.). The transplant studies at Berkeley and Cambridge showed that similar features are characteristic of *G. sarothrae*. Morphological variations between populations of a species correlated with environmental factors have been referred to as ecotypes. Turesson created the term ecotype, as an "ecological unit to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat" (Turesson, 1922). The fundamental idea embodied in the concept of ecotype is that the genotype best adapted to each particular environmental and edaphic situation is selected in each instance, and hence the species — "ecospecies" in the sense of Turesson — is formed by a series of such types. Although initially the term was defined strictly on an ecological basis, the definition was later modified by Turesson (1929) to include genetical criteria, and was simi-

FIG. 12. See legend p. 103.

larly interpreted by Clausen, Keck & Hiesey (1940; Clausen, 1952). The ecotype concept presupposes a mosaic-like ecological situation formed by patches of more or less discrete and uniform conditions both in time and space to which each ecotype is adapted, and envisages a situation, where a certain phenotype and/or genotype or group of similar phenotypes and/or genotypes, which presumably are those best fit to a given place, are consistently being selected over any others.

Gregor (1939, 1944) working with *Plantago maritima* along the coastal areas of Great Britain found that when the habitats in which this species grows are subjectively arranged in an ecological sequence, the populations within these habitats show a continuous variation between extremes in growth habit. A situation such as this has been designated by Huxley (1938) as a "cline." Clausen (1952) feels that clines are accidents of sampling and/or the result of field rather than garden measurements, and that the term cline should be used only when referring to individual characters. However, it is true that environmental situations form a highly complicated picture in nearly every instance. The more divergent two habitats occupied by a particular species, the easier it will be to detect ecotypes, and the more gradual the change from one into another, the easier it will be to see clines. To a certain extent both concepts can be considered accidents of sampling. But even if an environment composed of discrete patches of uniform conditions in space and time did exist, no selection for a "type" adapted to these conditions would be possible in the presence of much gene flow from adjacent populations.

In the case of *G. sarothrae*, if plants from populations from opposite extremes of ecological conditions are considered, all the morphological and physiological characteristics necessary to place them into *bona fide* ecotypes can be detected; if a series of intermediate situations is added, and particularly if these are arranged in a subjective order, arguments for recognizing a cline are present. But if the totality of the variation is studied, it will be seen that the pattern is a highly complicated one, probably related to a

Fig. 12. Four week old seedlings grown under uniform conditions. Largest, smallest and average sized seedlings from seed gathered near Logan in northern Utah (3257); near Thompson in east-central Utah (3260), and in central New Mexico (3267) are shown. The bottom picture shows a comparison of these same plants with a seedling from California. Note discrepancy in growth rate among the various populations.

highly complicated environment, as we have seen. The concepts of ecotype and cline are therefore not applicable in this particular case.

VARIATION IN THE CENTER AND THE PERIPHERY OF THE RANGE

In most species of animals, populations toward the geographical center of distribution of the species are denser, that is, the individuals are spaced closer; they are more variable; and populations are more contiguous to each other (Mayr, 1963). The usual explanation is that populations in the center of distribution are better adapted ecologically and therefore more subniches are occupied, hence the greater variability (Mayr, 1945, 1963). Also two other forces supposedly play an important role in such situations: density dependent factors and gene flow. The first of these will favor a diversification into subniches; the second will contribute greatly to increase the amount of variability. The data for *G. sarothrae* do not show such a well marked pattern. If we take the coefficient of variability as a measure of the amount of variability present, populations in the geographical center, Colorado, Utah and New Mexico, are not significantly more variable than those around them; on the contrary, if anything they are less variable. The explanation for this is no doubt complex, but an important factor is the type of distribution. In animals, increased density of individuals in a population will result in losses of some individuals to neighboring populations with a resulting increase of gene flow. In plants, no direct loss of individuals to neighboring populations is possible, and increase in the production of seeds decreases per individual rather than increases after a certain density is reached, due to the smaller size of the plants, as experiments with crop plants have shown. Consequently there is never such a population pressure in plants as there is in animals. The other important component usually present towards the center of the geographical range of species, that is more contiguous populations, is not present in the case of *G. sarothrae.* As indicated above, the pattern of groups of small populations in isolated pockets is fairly uniform throughout the range of the species. Towards the center of the range in Utah, Colorado and New Mexico, a rugged terrain is combined with very dry atmospheric conditions, so that rather than being more hospitable, the center is perhaps less so. As a result of the even and wide spacing of populations throughout the range of the species gene flow is low and more or less uniform throughout the area of distribution. The similar degree of variability of the populations in the center and towards the periphery might be accounted for this way.

VARIATION AND ADAPTATIVE RADIATION

The relation of topography to patterns of evolution and speciation is an interesting one, but also a highly complicated one. A puzzling aspect is the lack of radiation into new habitats of the North American species compared to the South American representatives of the genus. Two of the North American species are annual, and they have diverged morphologically to a certain extent, particularly in the number of florets in a head which has increased, and also in the loss of the already reduced pappus of the ligulate florets. Beyond that there has not been much change between the annual and perennial species. All of the six perennial species of North America are very close and, aside from chromosome number, the differences between them are of degree rather than of kind. The South American species on the other hand have radiated into a series of new and different niches. All South American species are perennial, but they vary from the cushion forming *G. baccharoides* which grows at altitudes of 3,000 m. in the Andes, and is only 5 cm. tall; to the low, creeping *G. repens* of the Aconquija Mts. also at altitudes of 3,000 m.; to the shrubby *G. paniculata* of central Chile, one m. or more in height with woody stems sometimes 2 to 3 cm. in diameter; to *G. gilliesii* of central Argentina which is very similar to *G. sarothrae* but has white rather than yellow ligulate flowers. The ecological variation is matched by the morphological variation, with changes in leaf shape and size, habit, woodiness, color of flower, etc. having taken place.

Evidently either the South American species have had a longer evolutionary history, or their rate of evolution has been greater. Since the tribe *Astereae* is most probably of North American origin and furthermore since the close generic relatives of *Gutierrezia* are found only in North America, it does not seem likely that the genus has had a longer history in the southern lands. An explanation for the higher rate of evolution in South America can be found in the combination of available niches, higher recombination index due to polyploidy, and isolation. These elements have not been present in North America to the same degree as they have existed in South America. It is also possible that the extensive Pleistocene glaciation of North America played an important role, by pushing the species south and off the higher places in the mountains, but there is not enough information to elaborate on this idea.

INCIPIENT AND SIBLING SPECIES

Sibling species, morphologically identical but reproductively isolated, are well known among animals (for a detailed discussion see Mayr, 1963). Among plants they are difficult to define, due to the more complex systems of self-incompatibility present which assure outbreeding. This makes testing for reproductive isolation much more difficult. Furthermore, in plants there often are modes of reproductive isolation between species other than genetic sterility, such as ecological isolation. As an example, in a population a single individual may be unable to breed with as much as one-half of all the plants present, while on the other hand, the individuals of two good sympatric species may be completely interfertile (Raven, 1962).

A mechanism which as a rule produces total reproductive isolation and which is independent of the self-incompatibility mechanism is polyploidy. Furthermore polyploidy is relatively easy to detect. Allopolyploids combine the characters of the two parental species while autopolyploids are morphologically and genetically similar qualitatively but not quantitatively. Segmental allopolyploidy stands in between allo- and autopolyploidy. All three types of polyploids to a certain extent, but particularly autopolyploids, may give rise to sibling species. Autopolyploid plants can be readily obtained artificially, and have been observed to occur naturally. As a rule they are highly sterile, due to the formation of multivalent associations at meiosis. For this reason fertile natural polyploids are usually assumed to be allopolyploids. Such an assumption has frequently been shown to be correct when the plants were investigated in detail.

The taxonomic treatment of the diploids and tetraploids will depend to a certain extent on the species concept that is adopted. According to a definition based primarily on morphology, diploids and tetraploids when morphologically alike have to be treated as one species; on the other hand, if a definition based primarily on the degree of crossing in nature is adopted, the two different levels of ploidy are better treated as separate species, when cytogenetical considerations indicate that there is no effective exchange of genes between them as is the rule.

The interpretation of particular situations is, nevertheless, more complex than this simple analysis would suggest, due to the high degree of variability of biological entities and the small amount of effective interbreeding between allopatric populations.

On account of their lack of mobility and their method of dispersal, plants have to be able to adapt to a variety of microenvironmental conditions. This is particularly true for perennial plants which are exposed to a variety of seasonal changes. Under these conditions selection favors systems which are flexible enough to compensate phenotypically for the differences from the paternal environment which the progeny will encounter. In addition selection will also favor the fixation of characteristics which are of general adaptive advantage to the population. The tremendous variation present in species of plants, and the lack of a definite pattern, is often perplexing. In *Gutierrezia sarothrae* a pattern of variation and distribution is present which represents an intermediate situation between total isolation and free gene exchange between populations. Both distance and pollinators effectively prevent cross-breeding between populations but there still can be some gene exchange due to blowing in of fruits from neighboring areas. Certain groups of populations, particularly those in California are completely isolated, and it is here that some of the extremes of variation are found, and it is also in California that the polyploid *G. bracteata*, a closely related species morphologically distinct from *G. sarothrae* has evolved (Solbrig, 1960, and unpublished). The diploid populations can best be regarded as forming a large, polytypic species. The treatment of the polyploid populations is more problematic.

The range and mean of the measurements of 850 diploid and 250 tetraploid plants of *Gutierrezia sarothrae* taken as a group are shown in table 10. There is a considerable amount of overlap in the range of diploid and tetraploids in each

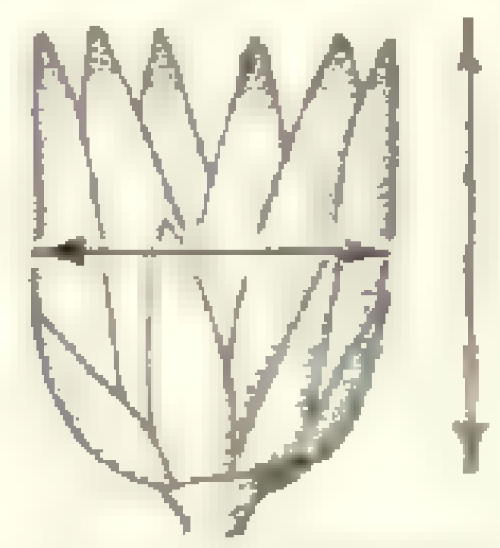
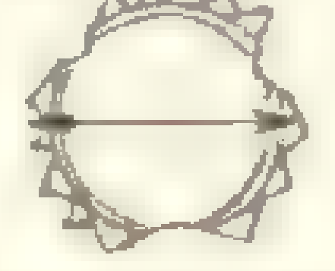
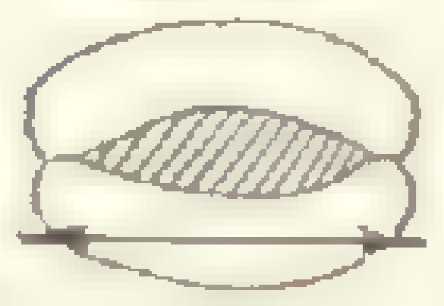
CHARACTER EXAMINED		RANGE		MEAN		t
		DIPLOID	TETRAPL.	DIPLOID	TETRAPL.	(P 0.05 = 1.96)
 PLANT HEIGHT		4 - 38	4.5 - 28	10.93	10.13	0.942
 INVOLUCRE	HEIGHT	2.5 - 5.0	2.6 - 6.2	3.77	3.56	0.075
	WIDTH	0.9 - 2.9	1.1 - 2.7	1.77	1.81	0.031
 FLOWER NUMBER	DISK	0 - 7	0 - 7	3.67	3.90	1.118
	RAY	2 - 7	3 - 6	4.87	4.49	0.851
 PAPPUS LENGTH	DISK	0.5 - 2.0	0.6 - 2.0	1.24	1.31	0.076
	RAY	0.2 - 1.2	0.4 - 1.3	0.58	0.73	0.333
 POLLEN DIAMETER		9 - 16	11 - 17	12.57	13.59	2.930
 STOMA LENGTH		14 - 24	15 - 25	18.13	19.97	1.870

TABLE 10. Comparison between diploid and tetraploid plants. Data from all populations have been added. (n = 250 tetraploids and 1350 diploids).

instance, and although the mean of the polyploid group tends to be greater, only pollen and stoma measurements show any appreciable mean difference. Significance tests show the difference to be significant only in the case of pollen diameter, at the 5% but not at the 1% level. On the basis of the characters analyzed, no plant taken at random can be placed with certainty as a diploid or as a tetraploid.

The pattern does not differ appreciably if we compare the same characters on a population basis, since there is still quite an overlap between diploid and tetraploid populations. The amount of overlap and the pattern differs with the character under consideration (see under morphological analysis and eco-geographic differentiation). From the morphological analysis, it is clear that in the *G. sarothrae* complex no separation into morphological categories is possible. Since the diploid and tetraploid populations are most probably reproductively isolated, they can be regarded as sibling species.

It is impossible to know at present whether the tetraploids in this group are descendants from a common ancestor or whether they had independent origins. Nevertheless, their scattered distribution and morphological differences seem to favor an independent origin for at least some of the populations. It is very possible that the Arizona populations, for example, are all of the same stock, but it is unlikely that the tetraploids from Grand Junction, Colorado, had the same origin. An independent origin could explain the differences between different tetraploids and between them and the diploids, particularly if we assume that the diploids of both small and large stature have independently given rise to tetraploid plants. We could easily have a tetraploid plant showing an increase in size over its small diploid progenitor, but still being smaller than some of the large diploid plants. The large tetraploid plants would of course have originated from large diploid plants. Most of the tetraploid populations are separated by considerable distances and consequently they are reproductively isolated from each other. The question arises as to whether these reproductively isolated populations which probably had an independent origin from different diploid parents could reasonably be considered to be one species. It is possible that some or all of the polyploid populations may evolve further and become morphologically distinct, as has been the case with *G. bracteata.* In such an eventuality there is no doubt that they will form separate species. In the meantime, I think it is legitimate to consider all the polyploids and diploids as part of one species with the polyploids polyphyletically tied into it. The present situation is similar to the problem presented when in the course of time several populations cross a threshold of difference into what is considered as a new, more advanced species. The principal difference is that the tetraploid populations of *G. sarothrae* have crossed the threshold suddenly and not gradually.

AUTOPOLYPLOIDY AND ALLOPOLYPLOIDY

A more difficult problem is to determine whether the polyploids are allopolyploids, segmental allopolyploids or autopolyploids. The absence of closely related diploid species and the morphological similarities between diploids and tetraploids almost certainly precludes interspecific allopolyploidy. On the other hand only the study of certain crosses can tell us if we are dealing with autopolyploidy or segmental allopolyploidy.

Polyploidy is a rather common phenomenon in plants, and in *Gutierrezia* it is very widespread. Out of the 12 species of the approximately 20 in the genus for which we have chromosome counts, 9 (75% of those with counts), are polyploid. Morphological analysis of the chromosomes indicates no noticeable change in the structure of the basic karyotype in the polyploid species analyzed (Rüdenberg & Solbrig, 1963). Unfortunately, no tetraploid population of *G. sarothrae* has been available for a similar study, but the closely related *G. bracteata* (n = 8 & 12), as well as the more remotely related species *G. californica* (n = 12) and the South American *G. gayana* (n = 28), essentially repeat the basic karyotype of diploid *G. sarothrae*. The "diploidization" — that is the acquisition of diploid pairing behavior — of these species has apparently not been dependent on any gross structural change in the chromosomes, and it is probable that a similar situation exists in tetraploid *G. sarothrae*.

Autopolyploidy is a rare phenomenon and some authors have completely ruled it out as a factor in speciation. But autopolyploidy when not accompanied by gross morphological variation is detectable only when the chromosome numbers of a whole group of plants are investigated systematically. In such a survey of the tribe *Astereae* of the *Compositae* (Raven *et al.* 1960; Solbrig *et al.* 1964) a number of species were found to have polyploid populations. Although no detailed study has been made, it is possible that some of these polyploids are autopolyploids. In this connection, the importance of counting large numbers of populations of a species should be emphasized.

SUMMARY

The cytology, the morphological variation of 11 characters, and the pollinators, of 53 populations of *Gutierrezia sarothrae* have been studied. Diploid and tetraploid populations have been discovered and their morphological variability compared. The geographical distribution and ecology of the species have also been investigated. The pattern which emerges is that of a very variable species, covering a large territory and growing under a series of very different conditions. No clear ecotypes or clines could be discovered, and this is assumed to result from the mosaic environment in which the species grows. No absolute qualitative or quantitative morphological deviation exists between the diploid and

tetraploid populations, which may be considered as sibling populations. No definite conclusion can be made as to the exact origin of the tetraploids.

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APPENDIX

LOCALITIES OF *G. sarothrae* POPULATIONS STUDIED

2758. California. 2 mi. W. of Temecula on Hwy. 78. In a slight depression formed by a dry creek bed. Plants rather sparse.

2766. California. 8.5 mi. E. of Chula Vista on road to Dulzura, just below Otay Reservoir Dam. Near roadside.

2769. California. 1.6 mi. E. of Rancho Santa Fe on road to Escondido. In old wheat field, growing half way up a hill near a pond where the land had not been cultivated.

2792. Arizona. 19.6 mi. N. of Roosevelt Dam. Common at roadside and fields in slight depression in the valley.

2793. Arizona. ½ mi. N. of Jct. Payson-Phoenix road with Hwy. 488. Common.

2794. Arizona. 5 mi. N. of Payson. Very common under a good stand of Juniper.

2801. Arizona. 12.6 mi. W. of Ash Fork. Transition zone between open *Pinus ponderosa* forest and *Pinus cembroides-Juniperus communis* complex. Locally abundant.

2802. Arizona. 9.8 mi. W. of Seligman. In a depression muddy due to the recent rains. The plants restricted to the depression and surrounding area, although they are present in the rocky mts. surrounding the area.

2805. Arizona. 0.8 mi. W. of Hyde Park. Under *Juniperus communis* association. Growing sympatrically with *Gutierrezia microcephala.* No sign of hybridization.

2905. Oregon. 2.5 mi. E. of Grant Co. Museum in John Day, on an old dirt road. Abundant in dry wash.

2911. Idaho. 8.7 mi. S. of Hansen. Foot of rocky hills with sandy soil covered with sagebrush.

2912. Idaho. 8.7 mi. S. of Hansen. At roadside. Plants 500 yards away from pop. 2911, but in wetter spot.

3134. Wyoming. 17 mi. SE of Mountainview on dirt road to Lonetree. Small population near roadside; soil whitish and sandy.

3136. Utah. 16 mi. SE of Jct. Hwy. 44 and Diamond Mt. Rd., at junction with Diamond Valley Creek. On a hillside, under sagebrush.

3141. Utah. Western Outskirts of Salt Lake City in abandoned field on Hwy. 50.

3142. Arizona. Hwy. 91, 2 mi. S. of Utah-Arizona border. Common in spots near roadside.

3143. Utah. Hwy. 15, 9 mi. W. of Mt. Carmel Jct. Rocky hillside under *Juniperus* association.

3145. Utah. Red Canyon, just before Bryce Canyon Nat. Park. Mixture of *Pinus ponderosa* and *Juniperus. Gutierrezia* common along dry wash.

3150. Utah. Hwy. 54, 7 mi. S. of Boulder. Small pop. under *Juniperus*, abundant in places. Soil white-sandy, loose.

3151. Utah. Hwy. 24, 15 mi. S. of Jct. with Hwy. 6. Sagebrush community, sandy soil. *Gutierrezia* abundant in this spot, but absent in the area.

3153. Colorado. 1 mi. W. of Hwy. 50, 22 mi. S. of Grand Jct. Common in lava flow.

3161. Colorado. 12 mi. E. of Durango on Hwy. 160. Roadside population.

3169. New Mexico. 3 mi. S. of Jct. Hwy. 285 with 286. Juniper-Pine association. *Gutierrezia* common in the area.

3212. Texas. 1 mi. W. of Van Horn on Hwy. 80. Sandy-clay soil. Plants very common in fields and at roadsides.

3215. New Mexico. 12 mi. S. of Glenwood, on Hwy. 260. Extraordinarily large plants with glaucous stems.

3224. Nebraska. 2 mi. E. of Roscoe, 9 mi. E. of Ogallala. Growing on loose, sandy soil on bluffs, and in gullies; large population.

3228. Nebraska. 1 mi. N. of Lisco on road to Orlando. Sandy soil. abundant at roadside and in fields.

3231. Nebraska. 10 mi. S. of Chadron. On roadcut and little hill. Very dry sandstone; overdispersed here, rare elsewhere.

3233. South Dakota. Hwy. 385, 7 mi. S. of Oelvichs. In open field, growing in depression, occasional.

3236. South Dakota. Hwy. 16, 10 mi. N. of Rapid City, 1 mi. E. of Piedmont. In ditch.

3238. South Dakota. Hwy. 16, 10 mi. N. of Rapid City, and about 1-2 mi. E. of Hwy. and pop. 3236. Overdispersed population in open field depression.

3243. North Dakota. 8 mi. W. of Dickinson. Uncommon in this area; overdispersed population in roadside ditch.

3245. North Dakota. 12 mi. N. of Bellfield on Hwy. 85. Growing in roadside ditch.

3246. North Dakota. Bridge over Little Missouri river and Hwy. 85. Badlands; small population.

3248. Montana. Hwy. 10, 2 mi. S. of Glendive. Roadside population.

3249. Montana. Hwy. 10, 20 mi. S. of Glendive. Roadside population; fairly common along roads and ditches.

3250. Montana. 3 miles E. of Sanders. Growing on Hwy. embankment.

3252. Wyoming. West outskirts of Sheridan. Growing on rocky hillside.

3254. Idaho. 12 mi. E. of Dubois, on dirt road to Kilgore. Growing on very weathered volcanic field with sagebrush; overdispersed locally, but generally rare.

3255. Idaho. Hwy. 91, 10 mi. S. of Pocatello. Very abundant in large rocky field at both sides of road; plants very uniform.

3256. Utah. Hwy. 91 between Logan and Ogden, 29 mi. S. of Ogden. Rocky summit; overdispersed population.

3258. Utah. 16 mi. N. of Vernal on Hwy. 44. On rocky overhang; very common in overdispersed population.

3259. Utah. Hwy. 134, 1½ mi. S. of Talmadge. Common in wash.

3260. Utah. Hwy. 50, 4 mi. W. of Thompson. Overdispersed population along Hwy., growing on loose, sandy soil.

3261. Colorado. ½ mi. before W. entrance to Colorado Nat. Mon. In roadside field; sandy soil; Juniper association.

3262. Colorado. Colorado Nat. Mon., 1 mi. N. of campground. Growing on eroded red sandstone; common in area.

3263. Colorado. Hwy. 50, 15 mi. W. of Salida. At roadside; locally very rare.

3264. Colorado. Dry hills W. of Fountain. Locally abundant.

3265. Colorado. 5 mi. S. of Trinidad on road to Raton. Juniper-piñon pine open association. Very common in fields and roadside.

3266. New Mexico. Gallinas canyon, 10 mi. W. of Las Vegas on Hwy. 65. On rocky cliffs and road embankments.

3269. New Mexico. Hwy. 285, 20 mi. N. of Roswell. In small wash, both at roadside and in fields; red, sandy soil; population very dense.

3270. New Mexico. 3 mi. S. of White City on Hwy. 62-180. Common in roadside and fields, loose sandy-clay soil.

3271. Texas. 23 mi. S. of White City, N. M., on Hwy. 67-180. Growing on rocky, limestone soil; very common.

3273. Texas. Hwy. 54, 30 mi. N. of Van Horn. In dry wash; soil sandy.

3280. Texas. 7 mi. E. of Alpine on Hwy. 67. Overdispersed population; locally common.

3282. Texas. Hwy. 67, 6 mi. W. of McCamey. Roadside population.

3283. Texas. Hwy. 67, 12 mi. W. of San Angelo. Common at roadside and in fields.

3284. Texas. Hwy. 67, 9 mi. W. of San Angelo. On roadbank and fields; abundant.

3286. Texas. 5 mi. W. of Abilene State Park, on road leading to Hwy. 277. Around and under oaks and Junipers; overdispersed but not too abundant.

3287. Texas. Hwy. 254, 5 mi. W. of Craford, Terry Co. In sandy-rocky, eroded wash.

3288. Texas. 2 mi. N. of Childress. Growing in abandoned field; overdispersed.

3289. Oklahoma. Hwy. 62, 11 mi. W. of Altus. On mezquite-cactus land; soil red, sandy; overdispersed and common in patches.

3290. Oklahoma. 4 mi. E. of Clinton, on Hwy. 66. On field next to road.

3291. Oklahoma. Hwy. 281, 9 mi. S. of Bouse Jct. On eroded red sandstone; in roadside cliffs and fields.

3292. Kansas. Hwy. 281, 10 mi. S. of Medicine Lodge. Rare locally; growing on eroded red sandstone in creek bed.

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THE FERNS OF PERU

CONTENTS

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INTRODUCTION

Nearly ten years ago I undertook the preparation of a manual of the Fern Flora of Peru with the encouragement and active support of the late Theodore K. Just of the Chicago Natural History Museum. This work has occupied a considerable portion of my time since then and although it is still far from complete I have decided to bring out the portion that has been finished. The principle reason for offering this partial account is the general need for modern literature on tropical American ferns and especially on the species-rich Andean region from Bolivia to Colombia.

The present portion treats the species of seven tribes of the Polypodiaceae. These tribes are represented by 33 genera and 176 native species. This is probably about a third of the genera of Pteridophyta to be found in Peru and about a quarter of the species. Three introduced species are also treated and eight that are to be expected in Peru, one of these in an additional genus.

The scope of the treatment and the method of study of each genus has been to some extent dictated by convenience. In the smaller genera I have considered all of the American material and the Peruvian species have been treated in relation to this study of broad scope. In such genera I have sometimes also included species related to the Peruvian ones, or those that may be expected to occur in Peru. In the larger genera, and especially where difficult problems were encountered, I have limited my study to the Peruvian species, although not to Peruvian material only. The generic descriptions have sometimes been limited, in some characters, to the Peruvian species.

Each genus has been treated in a monographic manner but I have felt it necessary to accept tentative conclusions when a problem went too far beyond the scope of the immediate study. I have tried to determine the type of each name and to see the holotype, when possible, or at least other authentic material. In most cases this effort has been successful; I have examined the holotype or an isotype of about

80 per cent of the basionyms and photographs or other authentic materials for an additional 10 per cent. I have made no attempt to include a full synonomy under each name, but have usually limited it to those names based on Peru material and the commonly used synonyms. In a few cases, where I have examined a type of an obscure name, I have included that also.

The classification adopted is essentially that of Carl Christensen as set forth in Verdoorn, Manual of Pteridology (1938). This has been modified in some places by more recent studies. I have not made a special study of generic problems but have followed a conservative course unless the need for a change and a proper solution have both been clear. I can not accept the present tendency to divide the Polypodiaceae into many families. The category of family loses its utility when restricted to groups of more or less closely related genera; such groups are better treated as subfamilies or tribes.

The principle collections of Peruvian ferns are in the Herbarium of the Chicago Natural History Museum, the United States National Herbarium (Smithsonian Institution) and the Gray Herbarium and it is on these collections that my work is largely based. Other important collections are in the Herbarium of the New York Botanical Garden, the Herbarium of the University of California (Berkeley), the Herbarium of the Missouri Botanical Garden and the Herbario San Marcos, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, and I have also consulted these. Type specimens, especially, have been studied at the Botanical Institute of the Academy of Sciences, U. S. S. R., Leningrad, the Paleobotanical Department, Naturhistoriska Riksmuseum, Stockholm, the Botanisches Museum, Berlin-Dahlem, the Muséum National d'Histoire Naturelle, Paris, Royal Botanic Gardens, Kew and the British Museum (Natural History). I am indebted to the officers of all of these institutions for the loan of materials or for the privileges extended during periods of study.

I have been aided in this work by many persons. Especial thanks are given to Alice F. Tryon who has assisted in many ways, including the preparation of the treatments of the genera *Jamesonia*, *Eriosorus* and *Pellaea* and to my several friends in Peru who were most helpful during my field work there and who have continued to send material to me: Dr. Ramón Ferreyra, Dr. César Vargas, Dr. Oscar Tovar, Dr. Emma Cerrate and the late Dr. Pedro Coronado. Dr. Karl Kramer has done much of the work on the treatment of *Lindsaea*. A. Sagástegui and A. López (Trujillo), S. G. E. Saunders (Lima) and P. C. Hutchison (Berkeley) continue to send valuable collections. The illustrations have been prepared over a period of time and by several artists. Mrs.

Bernedette Velick, Mrs. Joyce Todd, and Mrs. Alice Tryon have prepared the illustrations for about half of the species and Mrs. Ruth Chen the remainder. Mrs. Vivian Clement drew most of the habit sketches.

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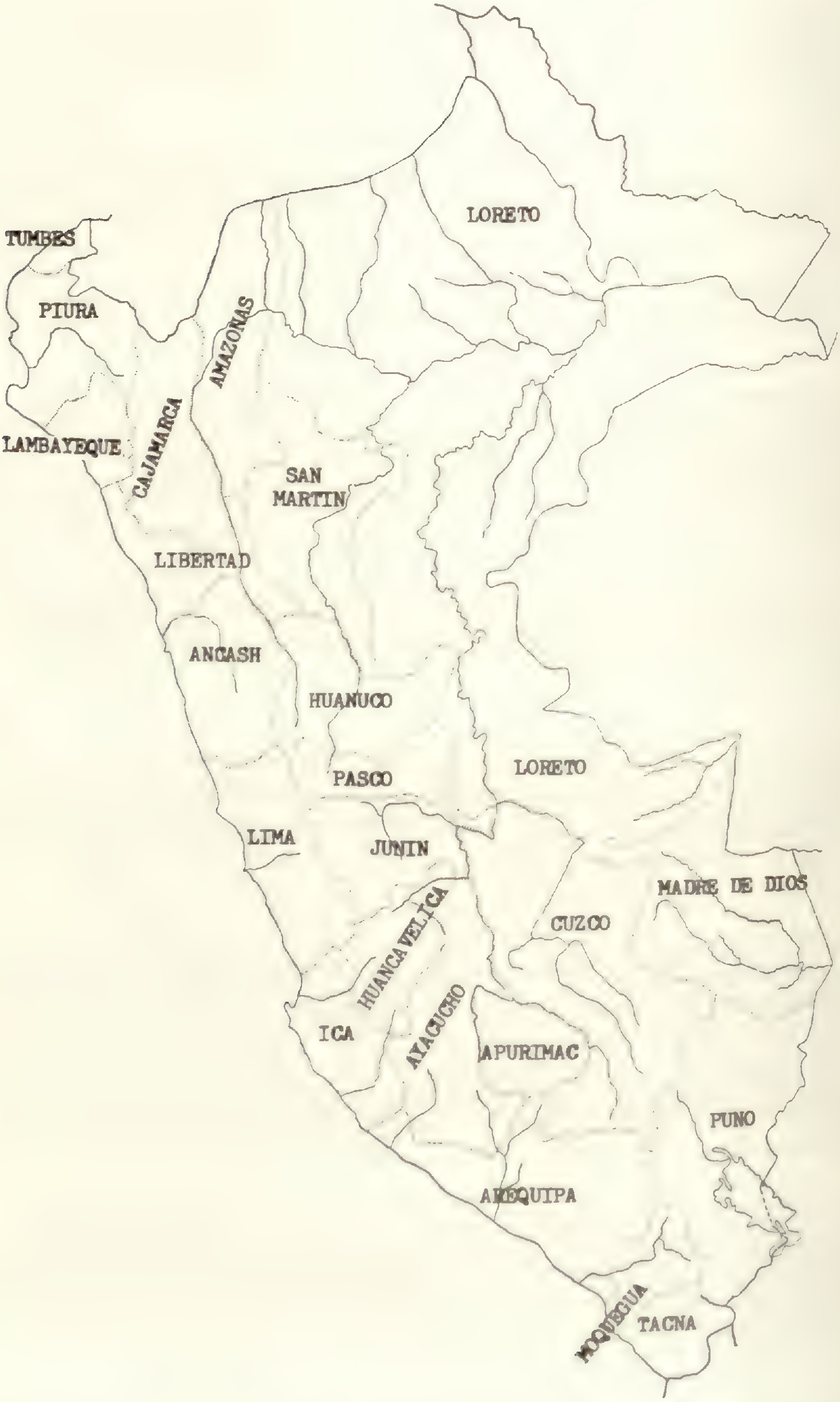
GEOGRAPHY

Some brief comments on the distribution of Peruvian ferns are presented here, accompanied by a map of the Departments, so that the information on habitat and range of each species may have some meaning to those unfamiliar with the country. The distribution maps do not always clearly show the general relation of the species to the type of vegetation in which it grows. This is due to the intricate system of deep valleys and high mountains, that is characteristic of the eastern Andes, and to the penetration of some of the larger rivers in deep valleys well into the central Andean region. It is commonplace to have a difference in elevation of some 2000 to 3000 m. within a relative few miles. Dots on a small scale map can not differentiate the major environments and vegetation types that may occur in one rather small area. The maps, then, must be interpreted in relation to the habitat and altitude given for the species and this information will distinguish between the species of the low valleys and those of the adjacent high ridges and mountains. A somewhat fuller account of the distribution and ecology of the Peru ferns is to be found in Tryon, R. The Ecology of Peruvian Ferns, (Amer. Fern Jour. **50**: 46-55. 1960) where I also include the more important references on the vegetation of Peru.

There are four principal types of distribution of the ferns of Peru. These correspond to the areas of the principal types of vegetation: the Lomas, the Sierra Steppe and Scrub, the Ceja and the Montaña.

The lomas are locally green areas on the coastal foothills of the Andes (from La Libertad southward) where fog, mist and occasionally rain are concentrated sufficiently



The Departments of Peru.

during the winter season so that a vegetation is developed in most years. During the summer the lomas are continuously dry. These are the only places in this part of the coast of Peru, below about 2500 m., in which ferns grow naturally. A few species have become naturalized along ditches or in other areas that are locally moist due to irrigation. Although none of the species treated here are confined to the lomas, some of them do occur there. The lomas are an important part of the range of *Adiantum subvolubile*, Map 32, and of *A. digitatum*, Map 36.

The Sierra Steppe and Scrub forms the vegetation of central Peru; it occurs in a broad area in Puno and diminishes northward through Junín and Huánuco into Cajamarca. The region, the Altiplano, is mostly above 3400 m. and is generally rather dry although many local mesic habitats occur. These latter are especially common in Cajamarca and northward where the typical Sierra vegetation is replaced by the wetter and somewhat lower Jalca. The most characteristic ferns of the Sierra Steppe and Scrub are the xeric species of *Cheilanthes*, *Notholaena* and *Pellaea*: *Cheilanthes scariosa*, Map 14; *C. pruinata*, Map 15; *Notholaena sinuata*, Map 19; *N. aurea*, Map 20; *N. nivea*, Map 22 and *Pellaea ternifolia*, Map 23. Species characteristic of locally mesic sites in this area are *Pityrogramma calomelanos* var. *ochracea* Map 9, *Adiantum Raddianum*, Map 33, and *A. Poiretii* var. *Poiretii*, Map 34. An extension of the Sierra fern flora on the Pacific side at a lower elevation is represented by some of the more common of the xeric species mentioned above and by two endemics: *Saffordia induta* (Map 26) and *Cheilanthes fractifera*. These latter species grow between 2500 and 3000 m. in a zone that is considerably drier than the higher elevations.

The Ceja vegetation occurs along the higher eastern slopes and high ridges of the Andes. In some areas clouds, fog and frequent precipitation afford cool and rather constantly moist conditions and here the vegetation forms a dense shrubby thicket. Two species of *Eriosorus*, *E. flexuosus*, Map 4, and *E. elongatus*, Map 5, are predominantly in this area. In most places in the eastern Andes, however, there is a gradual transition from the Sierra Steppe and Scrub vegetation to the lower Montaña (the forest). Such species as *Cheilanthes Poeppigiana,* Map 17, and *C. marginata,* Map 18, are characteristic of this region.

Below the Ceja vegetation the rainfall is greater, and with lower elevation the temperature increases. All of this eastern part of Peru is covered by the forested Montaña which includes all of the Departments of Amazonas, Loreto and Madre de Dios and portions of adjacent Departments. This is the richest area for species of ferns and although it has not been adequately collected, it seems clear that most species do not grow throughout the region. It is difficult to make clear distinctions within the fern flora but at least two rather typical types of range can be recognized. One is that of the upper elevations, above 1800 m. where there is generally greater relief, higher rainfall and cooler temperatures. Species that center in this region are *Adiantum peruvianum,* Map 27, and *A. macrophyllum,* Map 29. Those more characteristic of the lower elevations are *Saccoloma inaequale,* Map 2, *Pityrogramma calomelanos* var. *calomelanos,* Map 7, *Adiantum obliquum,* Map 30 and *A. latifolium,* Map 31.

A small area in the northern Department of Tumbes is forested but the fern flora is not sufficently known to relate it with the Montaña region, although several Montaña species grow there. Some species, such as *Adiantum Alarconianum,* are known in Peru only from this part of Tumbes.

Prior to 1944 the Department of Pasco was a part of Junín. I have not attempted to disentangle the many Junín collections that were made in what is now Pasco but have cited collections under the younger Department only when it was given on the label. Some of the maps do not show the location of a few cited collections, since these were received after the blocks had been prepared.

SYNOPSIS OF THE POLYPODIACEAE

The following synopsis and key include the 57 genera of Polypodiaceae that I know grow in Peru and some additional ones that may be expected to occur there. Certain rare endemics of adjacent countries have not been included. The genera included in the present portion are numbered as in the text, and the number of species in Peru is enclosed in parentheses; the genera that are not treated have not been numbered.

Tribe 1. Woodsieae

Woodsia, Hypoderris, Cystopteris.

Tribe 2. Dryopterideae

Dryopteris, Thelypteris, Ctenitis, Polystichum, Cyclopeltis, Didymochlaena, Tectaria, Polybotrya, Bolbitis.

Tribe 3. Asplenieae

Athyrium, Diplazium, Asplenium.

Tribe 4. Blechneae

Blechnum, Stenochlaena.

Tribe 5. Dennstaedtieae

1. Dennstaedtia (9), 2. Microlepia (0), 3. Saccoloma (2), 4. Hypolepis (5), 5. Blotiella (1).

Tribe 6. Cheilantheae

6. Eriosorus (9), 7. Jamesonia (9), 8. Pterozonium (1), 9. Pityrogramma (6), 10. Anogramma (1), 11. Gymnopteris (2), 12. Hemionitis (1), 13. Trachypteris (1), 14. Ceratopteris (1), 15. Cheilanthes (15), 16. Notholaena (13), 17. Pellaea (3), 18. Doryopteris (5), 19. Saffordia (1), 20. Adiantum (39).

Tribe 7. Pterideae

21. Pteridium (1), 22. Paesia (1), 23. Lonchitis (1), 24. Histiopteris (1), 25. Pteris (20), 26. Acrostichum (1).

Tribe 8. Vittarieae

27. Hecistopteris (1), 28. Vittaria (8), 29. Ananthacorus (1), 30. Polytaenium (4), 31. Anetium (1).

Tribe 9. Davallieae

32. Nephrolepis (6).

Tribe 10. Lindsaeeae

33. Lindsaea (10).

Tribe 11. Oleandreae

34. Oleandra (3).

Tribe 12. Polypodieae

Platycerium, Polypodium, Dicranoglossum (Eschatogramma).

Tribe 13. Elaphoglosseae

Peltapteris (Rhipidopteris), Microstaphyla, Elaphoglossum.

KEY TO THE GENERA OF POLYPODIACEAE

In the following key I have tried to use the generic characters whenever possible and when they are adequately known. However, I have also been guided by convenience of identification, and characters that may be readily seen or that may be expected on most specimens have been given some preference. In certain poorly defined genera, such as *Pellaea, Cheilanthes* and *Notholaena,* I have keyed out only the species that grow in Peru.

a. Sporangia not covered by a true indusium nor by a more or less modified portion of the margin (although the latter is sometimes present in nos. 7, 15 and 16). .... b.
  b. Sporangia borne continuously all over the lamina or segment, or a large area of it. .... GROUP I .... p. 10
  b. Sporangia borne only on the veins in definite clusters, lines or narrow bands (in no. 31 also sparsely scattered on the lamina surface), sometimes becoming contiguous at maturity. .... GROUP II .... p. 11
a. Sporangia covered or enclosed, at least when young, by a true indusium or by a modified portion of the margin (or by both). .... c.
  c. Sporangia borne on a usually continuous marginal commissure connecting the vein-ends (in no. 14 sometimes also solitary on other veins), or on a long commissure between the margin and the costa. .... GROUP III .... p. 14
  c. Sporangia borne at the ends of free veins which are not or only slightly extended laterally, or in sori on the free or areolate veins. .... d.
    d. Indusium formed wholly by the modified margin, or by a modified marginal lobe and a true indusium, these separate to fully joined. .... GROUP IV .... p. 15
    d. True indusium back from the margin which is not modified in relation to the sorus. .... GROUP V .... p. 16

GROUP I

a. Venation fully areolate. .... b.
  b. Lamina and its segments with several principle veins, stellate-pubescent; epiphyte. .... PLATYCERIUM
  b. Lamina and its segments with a single principle vein, or vascular axis, not stellate-pubescent; terrestrial. .... c.
    c. Fertile and sterile lamina with the lower surface densely covered with imbricate scales. .... 13. TRACHYPTERIS .... p. 86
    c. Fertile and sterile lamina with few or no scales on the lower surface. .... d.
      d. Rhizome large, erect; sterile pinnae finely areolate without dominant lateral veins (or groups of them), fertile pinnae abundantly paraphysate. .... 26. ACROSTICHUM .... p. 210

d. Rhizome creeping; sterile pinnae (or the sterile lamina) rather coarsely areolate, with definite lateral veins (or groups of them), fertile pinnae without paraphyses or with a few abortive sporangia. .... BOLBITIS

a. Venation open, or only casually areolate, or the veins connected only by a marginal strand. .... e.

e. Sterile lamina simple, entire, pinnately veined. .... ELAPHOGLOSSUM

e. Sterile lamina deeply lobed or more complex, or flabellately veined. .... f.

f. Fertile lamina entire or shallowly lobed, the sterile deeply pinnatifid or flabellately lobed or veined. .... g.

g. Sterile lamina flabellately lobed or veined. .... PELTAPTERIS

g. Sterile lamina pinnately lobed (deeply pinnatifid) .... MICROSTAPHYLA

f. Fertile and sterile lamina pinnate, 1-pinnate or more complex. .... h.

h. Pinnae not articulate, the fertile pinnae pinnatifid or more complex. .... POLYBOTRYA

h. Pinnae articulate, the fertile pinnae entire. .... STENOCHLAENA

GROUP II

a. Rhizome with trichomes (sometimes bristle-like with several inflated cells near the base). .... b.

b. Lamina 1-pinnate or more complex. .... c.

c. Lamina bipinnate or more complex, narrowly lanceolate to deltoid, or sometimes pinnate-pinnatifid and linear and the margins of the pinnae scarcely modified. .... 6. ERIOSORUS .... p. 40

c. Lamina pinnatisect to 1-pinnate, linear, pinnae entire to shallowly lobed, the margins ciliate or with a definite modified border. .... 7. JAMESONIA .... p. 53

b. Lamina entire, reniform to orbicular-cuneate. .... 8. PTEROZONIUM .... p. 64

a. Rhizome with scales (in no. 10 trichomes sometimes also present). .... d.

d. Lamina simple, entire; or furcate (dichotomously lobed) and the venation open. .... e.

e. Lamina furcate, dichotomously or subdichotomously lobed, small epiphytes (leaves ca. 1-2 cm. long) with open venation. .... 27. HECISTOPTERIS .... p. 211

e. Lamina simple, entire. .... f.

f. Sporangia borne continuously (or nearly so) along all the anastomosing veins (and sometimes also between them), or in two to several long lines. .... g.

g. Areolae in one series on each side of the costa. .... 28. VITTARIA .... p. 211

g. Areolae in two or more series on each side of the costa. .. h.

h. A single line of sporangia on each side of the costa. .... 29. ANANTHACORUS .... p. 219

h. Two or more lines of sporangia on each side of the costa, or sporangia along most of the veins. .... i.

i. Rhizome long-creeping; leaves herbaceous (fresh), papyraceous (dry), sporangia borne superficially and sparingly along the veins and also between them. .... 31. ANETIUM .... p. 224

i. Rhizome short-creeping; leaves coriaceous; sporangia borne in more or less depressed grooves, in several long lines or continuously along the veins. .... 30. POLYTAENIUM .... p. 220

f. Sporangia borne in roundish to long-oblong clusters on well defined portions of the veins. .... j.

j. Petiole not articulate, costa grooved and ridged on the upper side. .... THELYPTERIS

j. Petiole articulate near its base or at the rhizome, or not articulate and the costa more or less rounded on the upper side. .... POLYPODIUM

d. Lamina variously lobed to 1-pinnate or more complex, if dichotomously lobed then the venation areolate. .... k.

k. Venation areolate and the sporangia in lines or bands. .... l.

l. Lamina pubescent. .... 12. HEMIONITIS .... p. 84

l. Lamina scaly, at least beneath (sometimes the scales minute). .... m.

m. Lamina with dense imbricate scales beneath. .... n.

n. Sterile lamina spathulate (rarely lobed); sporangia borne on all veins. .... 13. TRACHYPTERIS .... p. 86

n. Sterile lamina more or less pedate; sporangia borne only on some veins in a narrow marginal band. .... 19. SAFFORDIA .... p. 133

m. Lamina with minute, appressed and scattered scales beneath. .... DICRANOGLOSSUM

k. Venation open, or if areolate, then the sporangia in definite round to elongate clusters. .... o.

o. Sori marginal, usually confined to the vein-tips but rarely extending about half-way down the veins. .... p.

p. Lamina glabrous, glandular, ceraceous or pubescent beneath. .... 16. NOTHOLAENA .... p. 105

p. Lamina scaly beneath. .... q.

q. Ultimate segments minute and subspherical; or the scales on the under surface of the pinnae strongly and irregularly dentate-ciliate, those on the upper side of the pinna-rachis linear. .... 15. CHEILANTHES .... p. 88

q. Ultimate segments moderately large and plane, the scales on the under surface of the pinnae finely pectinate-serrulate, or those on the upper side of the pinna-rachis filiform or substellately dissected. .... 16. NOTHOLAENA .... p. 105

o. Sori, or sporangia, dorsal, if reaching marginal vein-tips then extending all along the vein. .... r.

r. Sporangia in definite, round to elongated clusters, borne on a receptacle. .... s.
  s. Petiole articulate near its base or at the rhizome. .... POLYPODIUM
  s. Petiole not articulate. .... t.
    t. Rachis more or less rounded on the upper side, lamina usually pinnately lobed to pinnatisect (pinnae adnate), if 1-pinnate (or rarely more complex) then epiphytes and the pendent leaves with long patent, acicular trichomes. .... POLYPODIUM
    t. Rachis grooved and ridged on the upper side, or if more or less rounded, then terrestrial with erect to spreading leaves with articulate, catenate trichomes on the upper side of the axes (other types of trichomes sometimes also present). .... u.
      u. Upper side of rachis and pinna-rachises pubescent. .... v.
        v. Only short to long-acicular trichomes present on the upper side of the axes, these usually 1-celled and sometimes branched. .... THELYPTERIS
        v. Articulate, catenate, usually short and rufous trichomes present on the upper side of the axes, sometimes other types of trichomes also present. .... CTENITIS
      u. Upper side of rachis and pinna-rachises glabrous, glandular, scaly or with short to elongate, papilloid processes. .... w.
        w. Ultimate segments (pinnae or pinnules) equilateral or nearly so, not or hardly auriculate and not aristate, not toothed or with blunt teeth; lamina with few scales. .... DRYOPTERIS
        w. Ultimate segments (pinnae, pinnules or secondary pinnules) inaequilateral, auriculate or subauriculate, the apex and usually the auricle aristate, or the segment sharply toothed; lamina often densely scaly. .... POLYSTICHUM

r. Sporangia borne in long or short lines along the hardly modified veins. .... x.
  x. Segments hirsute on the upper surface (also on the lower surface and rachis). .... 11. GYMNOPTERIS .... p. 82
  x. Segments glabrous on the upper surface, or rarely deciduously pubescent and then the lower surface and rachis densely lanate. .... y.
    y. Perennial with well developed stem; rhizome scales rigid or firm, atropurpureous to light brown. .... 9. PITYROGRAMMA .... p. 65
    y. Annual with the stem poorly developed; rhizome scales thin, whitish, sometimes mixed with similar trichomes. .... 10. ANOGRAMMA .... p. 81

GROUP III

a. Leaves pedate, the primary segments adnate or joined at the base. .... 18. DORYOPTERIS .... p. 126

a. Leaves usually pinnate, rarely pedate and the basal pinnae sessile or stalked. .... b.

b. Venation wholly or partially areolate. .... c.

c. Aquatic; leaves thin, dimorphic, venation fully areolate-veined; stem poorly developed and short-lived. .... 14. CERATOPTERIS .... p. 87

c. Terrestrial, stem well developed and long-lived. .... d.

d. Rhizome with trichomes (no scales); sori borne in the sinuses of the segments and lobes. .... 5. BLOTIELLA .... p. 39

d. Rhizome with scales (trichomes sometimes also present in no. 24); sori borne along the sides of the segments, adjacent ones interrupted at the sinus (when present) unless it is very shallow. .... e.

e. Rachis flat to rounded, or only shallowly depressed, on the adaxial side, especially where the pinnae join; segments usually glaucous beneath; lower pinnae of larger leaves with stipule-like basal pinnules; rhizome slender and creeping. .... 24. HISTIOPTERIS .... p. 186

e. Rachis with a prominent and continuous groove on the adaxial side; segments not glaucous; the basal pinnules of the pinnae not stipule-like; rhizome erect or stout and creeping. .... 25. PTERIS .... p. 188

b. Venation wholly open, except for the veins connected by the fertile marginal commissure. .... f.

f. Segments dimidiate; fertile segments with a nearly unmodified, usually flat margin extending beyond the prominent indusium which opens outward; rhizome with scales. .... 33. LINDSAEA .... p. 235

f. Segments more or less equilateral. .... g.

g. Rhizome with trichomes (no scales); lamina glandular-pubescent or pubescent, at least beneath (rarely glabrous). .... h.

h. Primary and other rachises (toward their apex) and the larger costae with convex, often separate, lobes between the segments; inner indusium a more or less continuous membrane or reduced to a row of trichomes. .... 21. PTERIDIUM .... p. 181

h. Primary and other rachises and costae without lobes between the segments. .... i.

i. Inner indusium a well developed membrane; major axes of the leaf and usually the segments hard or firm, lamina usually glandular-pubescent, especially beneath, rhizome slender, hard, with dark firm trichomes. .... 22. PAESIA .... p. 184

i. Inner indusium absent, whole leaf succulent, sparingly covered with whitish crispate to flattened trichomes similar to those on the thick, fleshy rhizome. .... 23. LONCHITIS .... p. 186

g. Rhizome with scales (trichomes sometimes also present in no. 24); lamina glabrous to scaly beneath, not pubescent. .... j.

j. Fertile commissure marginal, the marginal indusium and the mature sporangia usually distant from the midrib, sori paraphysate. .... 24. HISTIOPTERIS and 25. PTERIS, see heads e.

j. Fertile commissure near the midrib (in narrow segments marginal or intramarginal), the indusium and the mature sporangia nearly or quite extending to it, sori not paraphysate. .... BLECHNUM

GROUP IV

a. True indusium present, separate from the opposed margin of the segment to fully joined with it and then forming a cup- or purse-shaped, or globular to cylindrical indusium. .... b.

b. Marginal lobe joined to the true indusium to form a symmetrical cup- or purse-shaped, or globular to cylindrical indusium; rhizome long-creeping, pubescent. .... 1. DENNSTAEDTIA .... p. 18

b. Marginal lobe separate, or nearly so, from the true indusium and exceeding it, sometimes slightly modified; rhizome erect, with scales. .... 3. SACCOLOMA .... p. 30

a. True indusium absent, sporangia covered by (or in no. 20, borne on) a modified and reflexed marginal lobe or band. .... c.

c. Sporangia borne on veins that extend into the modified margin. .... 20. ADIANTUM .... p. 135

c. Sporangia borne on veins that end in the leaf tissue back of the modified margin. .... d.

d. Rachis and pinna-rachises grooved on the adaxial side, the grooves interrupted (or nearly so) where the axes join. .... 4. HYPOLEPIS .... p. 32

d. Rachis and pinna-rachises grooved on the adaxial side, the grooves fully continuous where the axes join; or the rachis flat to rounded on the adaxial side, or the pinna-rachis absent. ...... e.

e. Petiole more or less straw-colored, or atropurpureous and the pinnae ternate. .... 17. PELLAEA .... p. 121

e. Petiole more or less reddish-brown to atropurpureous, the pinnae pinnate. .... f.

f. Lamina glabrous, glandular or ceraceous beneath, or loosely pubescent and the lower surface evident. .... 15. CHEILANTHES .... p. 88

f. Lamina scaly beneath, or densely tomentose and the lower surface concealed. .... g.

g. Lamina scaly beneath, the ultimate segments minute and subspherical, or the petiole scales ovate-lanceolate and the scales on the lower surface of the pinnae strongly and irregularly dentate-ciliate. .... 15. CHEILANTHES .... p. 88

g. Lamina pubescent beneath, or scaly and the ultimate segments moderately large and plane, the petiole scales linear-lanceolate, or the scales on the lower surface of the pinnae finely pectinate-ciliate. .... 16. NOTHOLAENA .... p. 105

GROUP V

a. Leaf, pinnae or pinnules articulate, deciduous (or easily detached in dried material). .... b.

b. Leaf or pinnae articulate; indusium orbicular, reniform or lunate. .... c.

c. Lamina 1-pinnate, pinnae simple, articulate; rhizome erect, often stoloniferous. .... 32. NEPHROLEPIS .... p. 225

c. Lamina simple, entire, leaf articulate near, or well above, the base of the petiole; rhizome extensively creeping or climbing. .... 34. OLEANDRA .... p. 244

b. Pinnules articulate, dimidiate; indusium elongate along the vein; lamina bipinnate, the upper side of the pinna-rachis with digitate processes at the base of the pinnules. .... DIDYMOCHLAENA

a. Leaf and its segments not articulate, persistent. .... d.

d. Indusium elongate, attached along the vein. .... e.

e. Rhizome scales clathrate (the lateral cell walls dark and much thickened, the top and bottom walls very thin and nearly colorless); pinnae (or pinnules) commonly strongly inequilateral at the base. .... ASPLENIUM

e. Rhizome scales with the cell walls more or less equally and moderately thickened, the top and bottom walls brownish; pinnae (or pinnules) equilateral or slightly inequilateral at the base. .... f.

f. Indusium about 3 to 4 times as long as broad; ultimate segments or lobes strongly toothed or laciniate. .... ATHYRIUM

f. Indusium about 10 to 20 (or more) times as long as broad, or shorter and the ultimate segments or lobes entire to shallowly toothed. .... DIPLAZIUM

d. Indusium usually about as long as broad, attached at essentially one point on the vein or receptacle (sometimes its two sides also attached to the leaf-tissue). .... g.

g. Indusium attached to the leaf-tissue on each side of the receptacle. .... h.

h. Rhizome with trichomes, long-creeping; indusium and lamina pubescent. .... 2. MICROLEPIA .... p. 29

h. Rhizome with scales, erect; indusium and lamina glabrous. .... 3. SACCOLOMA .... p. 30

g. Indusium attached only at the receptacle or vein. .... i.

i. Indusium scale-like or saucer-shaped to globose. .... j.

j. Indusium scale-like, attached at its base and arching over the sporangia; lamina bipinnate to tripinnate, thin, glabrous. .... CYSTOPTERIS

j. Indusium saucer-shaped to globose, of few to several segments attached around the receptacle. .... k.

k. Venation open, lamina with many pinnatifid to 1-pinnate pinnae; rhizome short-creeping. .... WOODSIA

k. Venation areolate, lamina with a large, entire, central segment, deeply lobed at the base to form two smaller pinna-lobes; rhizome long-creeping, (some indusia may be elongate). .... HYPODERRIS

i. Indusium peltate or reniform. .... l.

l. Upper side of the rachis (and pinna-rachises when present) pubescent; if the lamina is tripinnate or more complex then it is catadromous (the basal segment or branch on the basiscopic side) throughout. .... m.

m. Pubescence on the upper side of the axes wholly of short to long, acicular trichomes, these usually one-celled and sometimes branched. .... THELYPTERIS

m. Pubescence on the upper side of the axes wholly or partly of articulate, catenate, usually short and rufous trichomes. .... n.

n. Venation open. .... CTENITIS

n. Venation areolate. .... TECTARIA

l. Upper side of the rachis (and pinna-rachises when present) glabrous, glandular, scaly or with short to long papilloid processes; or pubescent and the lamina tripinnate or more complex and anadromous (the basal segment or branch on the acroscopic side) in the distal portions, or throughout. .... o.

o. Lamina 1-pinnate; pinnae simple, entire to crenate, the base truncate on the acroscopic side, prominently auriculate on the basiscopic side, the auricle curved and overlaying the rachis. .... CYCLOPELTIS

o. Lamina more than 1-pinnate; or 1-pinnate and the base of the pinnae nearly equilateral, or better developed on the acroscopic side. .... p.

p. Lamina less than tripinnate and the ultimate segments (pinnae or pinnules) equilateral or nearly so, not or hardly auriculate and not aristate; or tripinnate or more complex and the pinnae broadest at the base and the pinnules acute; lamina usually scaly but not densely so. .... DRYOPTERIS

p. Lamina less than tripinnate and the ultimate segments (pinnae or pinnules) inequilateral, auriculate or subauriculate, the apex, and usually the auricle, aristate; or tripinnate and the pinnae not or hardly broader at the base and the pinnules obtuse; lamina often densely scaly. .... POLYSTICHUM

POLYPODIACEAE

TRIBE 5. DENNSTAEDTIEAE

1. DENNSTAEDTIA Bernh. Jour. Bot. Schrad. 1800(2): 124. 1801. Type: *Trichomanes flaccidum* Forst. = *Dennstaedtia flaccida* (Forst.) Bernh.

Terrestrial, the rhizome slender and long-creeping, pubescent, bearing the leaves at usually wide intervals; leaves large to very large, 1-pinnate to quadripinnate-pinnatifid, glabrous or pubescent, veins free; sorus marginal, not paraphysate, the indusium formed of the inner (true) indusium and the outer, opposed lobe of leaf-tissue, these fully joined basally to form a reflexed saucer- to purse-shaped or globular to cylindrical whole which is bilabiate or not. — 11 American species.

Tryon, R. A review of the genus Dennstaedtia in America. Contrib. Gray Herb. 187: 23-52. 1960.

Most of the species grow in forests or along forest borders and have often long leaves that depend on the surrounding vegetation for support. All but two of the American species (*D. distenta* of Mexico, Central America and the Greater Antilles, and *D. punctilobula* of eastern North America) grow in Peru.

KEY TO SPECIES

a. Axis of the penultimate segments lacking perpendicular herbaceous wings on the upper surface, or perpendicular wings present but the one on the basiscopic side not decurrent onto the axis of the next order; trichomes on the under surface of the pinnules, when present, whitish to brownish and usually subopaque. .... b.

b. Sterile vein tips, on the upper surface, slender, ending well back of the glabrous margin; tertiary axes glabrous to sparsely or densely pubescent beneath with straight to tortuous, more or less spreading, trichomes; lower pinnae stalked with the basal pinnules not or not much reduced. .... c.

c. Many or most of the sori borne in a sinus; pinnules more or less pubescent beneath; lamina deltoid. .... 1. *D. cicutaria*

c. All or most of the sori terminal on lobes; pinnules glabrous to glabrate; lamina ovate-lanceolate to deltoid-lanceolate. .... 2. *D. glauca*

b. Sterile vein tips, on the upper surface, enlarged, clavate to punctate (rarely slender in *D. obtusifolia*); tertiary axes glabrate to usually subappressed, ascending pubescent beneath with the trichomes more or less curled. .... d.

d. Lamina pinnate-pinnatifid or more complex; the lower pinnae usually subsessile with the basal pinnules reduced. .... e.

e. Sterile veins ending well back of the glabrous margin. .... f.

f. Pinnules 1-pinnate to pinnate-pinnatifid, apical segments of the pinna separate or nearly so to the prolonged apex, the separate ones closest to the tip obtuse; obtuse pinnules on the apical pinnae deeply pinnatifid; lamina deltoid. .... g.

g. Mature sori, at least the basal acroscopic ones on an ultimate segment, mostly 1.0-1.5 mm. broad and about half as thick. .... 5. *D. dissecta*

g. Mature sori mostly 0.5-1.0 mm. broad and about as thick. .... 6. *D. obtusifolia*

f. Pinnules entire to deeply pinnatifid, apical segments of the pinna confluent back of the prolonged tip, the separate ones closest to the tip acute; obtuse pinnules on the apical pinnae entire to lobed; lamina evidently ovate. .... 7. *D. arborescens*

e. Sterile veins nearly reaching the persistently pubescent margin. .... 8. *D. Sprucei*

d. Lamina 1-pinnate, the pinnae entire. .... 9. *D. Wercklei*

a. Axis of the penultimate segments bordered on each side, on the upper surface, by a pronounced herbaceous wing perpendicular to the plane of the segment, the wing on the basiscopic side decurrent onto the axis of the next order either as an herbaceous wing or as a pronounced ridge; trichomes on the under surface of the pinnules wholly clear brown or tan (rarely subopaque or whitish). .... h.

h. Basal segments of the pinnules of the central pinnae usually subopposite to nearly opposite, rather or quite equal in size, the inferior not or slightly ascending; sori globular to less often subglobular or rarely cylindrical; lamina deltoid. ...... 3. *D. globulifera*

h. Basal segments of the pinnules of the central pinnae definitely alternate, quite unequal in size, the inferior ascending to strongly ascending; sori cylindrical to subcylindrical, rarely globular; lamina ovate to lanceolate-ovate. .... 4. *D. bipinnata*

1. **Dennstaedtia cicutaria** (Sw.) Moore, Ind. Fil. xcvii. 1857. FIG. 1, MAP 1.

Dicksonia cicutaria Sw. Jour. Bot. Schrad. 1800 (2):91. 1801. Type: Jamaica, *Swartz*, S-PA! fragment and photographs US!; isotype: Herb. Willd. 20156, B! photo GH.

Dicksonia rubiginosa Kaulf. Enum. Fil. 226. 1824. Type: Rio de Janeiro, Brazil, Herb. Mertens; isotype: LE! photo GH.

Dennstaedtia rubiginosa (Kaulf.) Moore, Ind. Fil. xcvii. 1857.

Leaf ca. 1-4 m. long, lamina deltoid, tripinnate to quadripinnate-pinnatifid; lower pinnae stalked and with the basal pinnules not, or not much, reduced, axes of the penultimate segments without herbaceous ridges or wings on the upper surface, sterile vein-tips (on the upper surface) slender, ending well back of the glabrous to sparingly pubescent margin; pinnules more or less pubescent beneath (as well as above) with whitish to brownish usually dimorphic trichomes, some one-celled, short, acicular, rigid, others (rarely the only kind) multicellular, longer, sometimes lax and subtortuous; most sori borne in a sinus, mature indusium saucer-shaped to purse-shaped.

In addition to the characters mentioned in the key, this species and the following one, *D. glauca,* may often be separated by the color of the major axes. In *D. cicutaria* they are usually brownish and in *D. glauca* they are usually straw-colored.

Central Mexico to Panama; Greater Antilles; Venezuela and Colombia to Bolivia and southern Brazil.

In dense or open forests or at the borders of clearings, Loreto and San Martín south to Puno, 200-1700 m.

Selected specimens: SAN MARTIN: near Tarapoto, *Spruce 4338* (GH, K), *4346* (K); Zepelacio, near Moyobamba, *Klug 3553* (F, GH, K, US). LORETO: mouth of Río Santiago, *Mexia 6128* (BM, F, GH, K, UC, US); La Victoria, Amazon River ("near Brazil"), *L. Williams 2620* (F). HUANUCO: Cotirarda (Dist. Churubamba), *Mexia 8218* (F, GH, UC, US); between Huánuco and Pampayacu, *Kanehira 168* (US); Pozuzo, *Macbride 4605* (F, US); Tingo María, *Tryon & Tryon 5261* (GH). PASCO: Quillasú, *Soukup 3513* (US). JUNIN: Colonia Perené, *Killip & Smith 25234* (F, US); La Merced, *Killip & Smith 23699* (F, GH, US); Chanchamayo valley, *Schunke 170* (F), *756* (F), *1351* (F, US); Satipo, Aug. 1940, *Ridoutt* (GH, USM). AYACUCHO: Estrella, between Huanta and Río Apurímac, *Killip & Smith 23072* (GH, US); Ccarrapa, between Huanta and Río Apurímac, *Killip & Smith 22440* (GH, US). CUZCO: Potrero, 8 km. w. of Quillabamba, *Tryon & Tryon 5372* (BM, F, GH, U, US, USM); Yanayacu, *Bües 2007* (US). PUNO: Churumayo, *Soukup 871* (F).

2. **Dennstaedtia glauca** (Cav.) Looser, Rev. Hist. Geog. Chile 69: 184. 1932. FIG. 2.

Davallia glauca Cav. Descr. 278. 1802. Type: Cordillera de Planchon, Chile, *Neé*, MA, fragment BM! (Looser, *loc. cit.*, and C. Chr. in Dansk. Bot. Ark. 9(3):28. 1937, discuss the identity of the type).

Dicksonia Lambertiana Remy, Gay, Fl. Chil. 6: 523. 1853. Type: Chile, Herb. Bonpland, P ? (not seen); isotype: K!

Dennstaedtia Lambertiana (Remy) Christ, Farnkr. 312. 1897.

Leaf ca. 0.5-2 m. long, lamina ovate-lanceolate to deltoid-lanceolate, tripinnate-pinnatifid to quadripinnate-pinnatifid; lower pinnae stalked, with the basal pinnules not or hardly reduced, axes of the penultimate segments with an herbaceous ridge on the upper surface, sterile vein tips, on the upper surface, slender, ending well back of the glabrous margin; pinnules glabrous or nearly so; sori predominantly terminal on lobes, mature indusia usually purse-shaped.

Specimens of the previous species, *D. cicutaria*, that are only slightly pubescent may be confused with *D. glauca*. The character of the sorus and especially that of the shape of the lamina, mentioned in the key, must then be employed for certain identification.

Chile, northeast to adjacent Argentina, north to Bolivia and southern Peru.

In moist, shrubby or rocky ravines and on banks, Cuzco and Puno, 2900-3700 m.

Specimens seen: CUZCO: Hacienda Chiraura, prov. Quispicanchis, *Herrera 2623* (UC, US); Quebrada de Quispicanchi, *Herrera 2598* (US); near Cuzco, *Herrera 8* (US); Cuzco, *Herrera 279* (GH, US); San Jerónimo, *Vargas 2320* (US); entre Lares y Hierbabunayoc, *Vargas 12011* (GH). PUNO: Cuyo-Cuyo, *Weberbauer 934* (B).

3. **Dennstaedtia globulifera** (Poir.) Hieron. Bot. Jahrb. 34: 455. 1904. FIG. 3.

Polypodium globuliferum Poir. Lam. Encycl. 5: 554. 1804. Type: Santo Domingo, Plumier, Fil. t. 30.

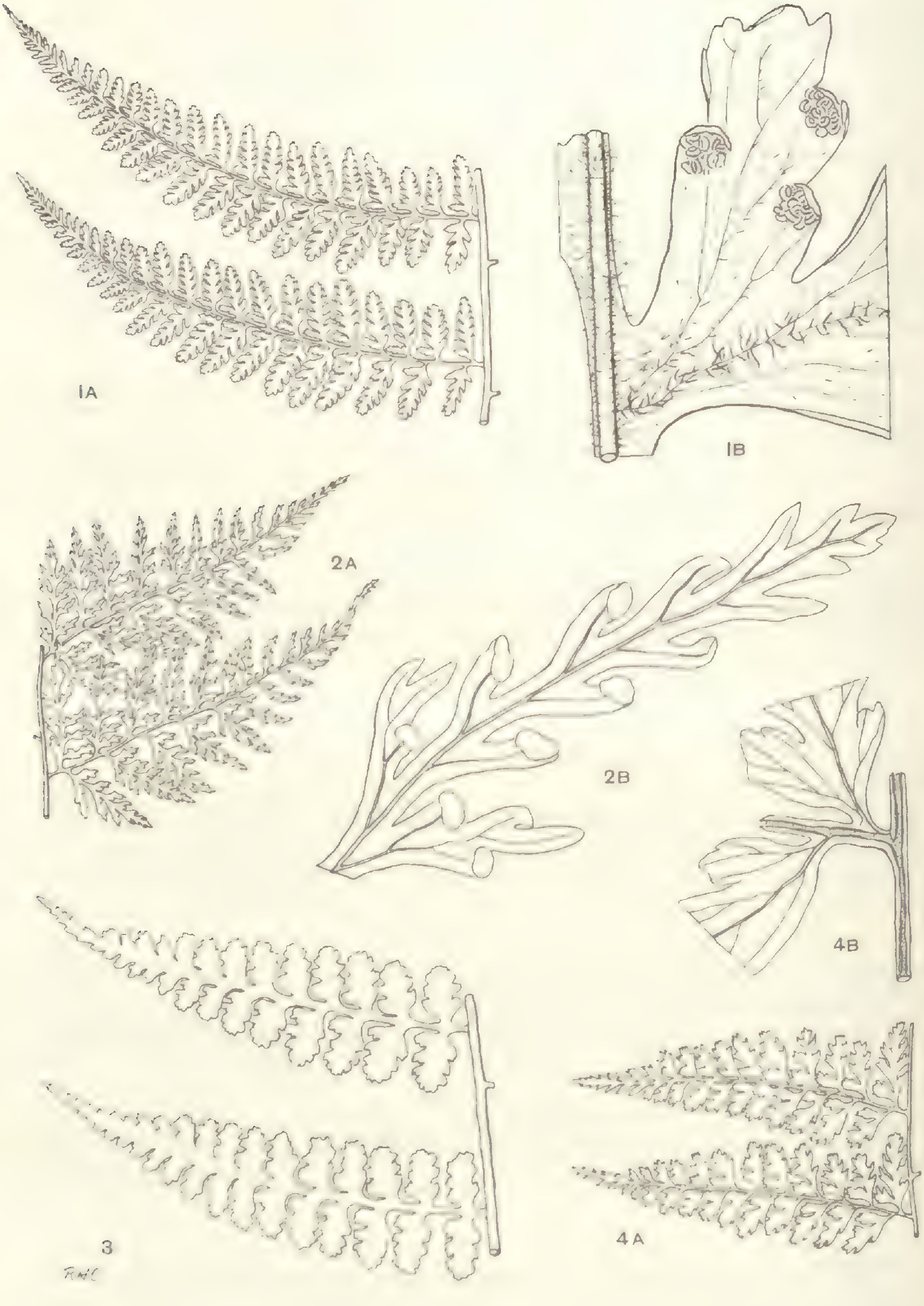
Dicksonia tenera Presl, Del. Prag. 1: 189. 1822. Type: Rio de Janeiro, Brazil, *Pohl 4062*, W! det. Presl, may be an isotype, an unannotated duplicate is at GH.

Dicksonia exaltata Kze. Bot. Zeit. 8: 59. 1850. Type: Santo Domingo, Plumier, Fil. t. 30. (nom. superfl., illegit.)

Dennstaedtia tenera (Presl) Mett. Ann. Sci. Nat. V, 2: 261. 1864.

Dennstaedtia exaltata (Kze.) Hieron. Bot. Jahrb. 34: 454. 1904. (illegit.)

Leaf ca. 1-3 m. long, lamina deltoid, tripinnate to nearly quadripinnate; lower pinnae stalked, with the basal pinnules not or scarcely reduced, basal segments of the pinnules of the central pinnae subopposite, nearly or quite equal in size, the inferior one not or slightly ascending, axes of the penultimate segments bordered on each side, on the upper surface, by a pronounced herbaceous wing perpendicular to the plane of the segment, the wing on the basiscopic side decurrent onto the axis of the next order, sterile vein-tips usually slender, ending well back of the glabrous margin; pinnules more or less pubescent beneath, the trichomes wholly clear brown or tan (rarely subopaque or whitish), rather straight and rigid; indusia globular to rarely cylindrical.



FIGS. 1-4. Fig. 1. *Dennstaedtia cicutaria:* A, pinnules, × ½, Haiti, *Leonard 4956*, GH; B, base of fertile tertiary segment, × 12, Mexico, *Conzatti & Gonzales 573*, GH. Fig. 2. *D. glauca:* A, pinnules, × ½, Chile, *Morrison 17076*, GH; B, fertile tertiary segment, × 6, Argentina, *Schreiter 5783*, GH. Fig. 3. *D. globulifera:* pinnules, × ½, Colombia, *H. H. Smith 1118*, GH. Fig. 4. *D. bipinnata:* A, pinnules, × ½, Bolivia, *R. S. Williams 1259*, GH; B, base of tertiary segments, × 5, Cuba, *Hioram 6299*, GH.

This species is rather closely related to the next, *D. bipinnata,* and the differences are discussed under its treatment. The distinctive characters of the basal segments of the pinnules are best developed in the central pinnae. In the apical pinnae, where the pinnules are small, the basal pinnules of the pinnae have the same characters. In the larger, lower pinnae both the basal and apical pinnules may be similar to those characteristic of *D. bipinnata.*

Texas; Mexico to Panama; Greater Antilles; Venezuela and Colombia south to Bolivia, Argentina and southern Brazil.

In forests, Cajamarca, Junín and Cuzco, 1000-1800 m.

Specimens seen: CAJAMARCA: Taulis, prov. Hualgayoc, *Koepcke 676* (GH); Prov. Hualgayoc, *Soukup 3809* (F, US). JUNIN: above San Ramón, *Killip & Smith 24648* (F, US); Pichis Trail, Yapas, *Killip & Smith 25473* (F, GH, US); La Merced, *Soukup 1076* (F); Chanchamayo valley, *Schunke 12* (F, US) Quebrada of Pariahuanca, *Mathews 974* (K). CUZCO: Valle de Occobamba, *Bües 879* (US).

4. **Dennstaedtia bipinnata** (Cav.) Maxon, Proc. Biol. Soc. Wash. 61: 39. 1938. FIG. 4.

Dicksonia bipinnata Cav. Descr. 174. 1802. Type: Porto Rico, *Ventenat,* MA; isotype: Herb. Willd. 20165-1, B! photo GH, fragment US! (Maxon, *loc. cit.,* discusses the Herb. Willdenow specimen accepted as an isotype).

Dicksonia adiantoides Willd. Sp. Pl. 5: 488. 1810. Type: Caripe, Venezuela, *Humboldt & Bonpland (466),* Herb. Willd. 20165-2, B! photo GH, fragment US!; isotype: Herb. Humboldt & Bonpland *(466),* P!

Dennstaedtia adiantoides (Willd.) Moore, Ind. Fil. xcvii. 1857.

Leaf ca. 1-3 m. long, lamina ovate to lanceolate-ovate, tripinnate-pinnatifid to quadripinnate-pinnatifid; lower pinnae stalked, with the basal pinnules not or scarcely reduced, basal segments of the pinnules of the central pinnae definitely alternate, quite unequal in size, the inferior ascending, axes of the penultimate segments bordered on each side, on the upper surface, by a pronounced herbaceous wing perpendicular to the plane of the segment, the wing on the basiscopic side decurrent onto the axis of the next order, sterile vein-tips usually slender, ending well back of the glabrous margin, pinnules usually slightly pubescent beneath, the trichomes often nearly confined to the base of the tertiary segments, trichomes wholly clear brown to tan (rarely subopaque or whitish), rather straight and rigid; indusium cylindrical to rarely globular.

D. bipinnata and *D. globulifera* often differ in characters other than those mentioned in the key. The lamina in *D.*

bipinnata is usually coriaceous or firmly herbaceous and is usually shining beneath. In *D. globulifera* the lamina is usually softly herbaceous and dull beneath. The ultimate segments of *D. bipinnata* are acutely to subacutely toothed while those of *D. globulifera* are entire to usually bluntly toothed.

Southern Florida; Mexico to Panama; Greater Antilles; Trinidad to Colombia, south to Peru and Bolivia.

In forests, Loreto, San Martín to Ayacucho, 135-1800 m.

Specimens seen: SAN MARTIN: Monte Campana, Tarapoto, *Spruce 4690, 4890* (K); San Roque, *L. Williams 7179* (F). LORETO: mouth of Río Santiago, *Mexia 6127* (BM, F, GH, K, UC, US); Puerto Arturo, below Yurimaguas, *Killip & Smith 27796* (US); Maynas, 1831, *Poeppig* (K). JUNIN: Satipo, Aug. 1940, *Ridoutt* (GH, USM); Chanchamayo valley, *Schunke 145, 945* (F), *947* (F, US); La Merced, *Soukup 1027* (F); Cahuapanas, Río Pichis, *Killip & Smith 26799* (US); Colonia Perené, *Killip & Smith 25188* (US). AYACUCHO: near Kimpitiriki, Apurímac valley, *Killip & Smith 22875* (F, US), *22987* (BM, US); Estrella, between Huanta and Río Apurímac, *Killip & Smith 22651* (GH, US).

5. **Dennstaedtia dissecta** (Sw.) Moore, Ind. Fil. 305. 1861. FIG. 5.

Polypodium dissectum Sw. Prod. 134. 1788, not Forst. 1786.

Dicksonia dissecta Sw. Jour. Bot. Schrad. 1800 (2): 91. 1801. Type: Jamaica, *Swartz*, S-PA! photo and fragment US!

Dicksonia cornuta Kaulf. Enum. Fil. 227. 1824. Type: Brazil, "ex Spreng." (Brazil, *Sello*, B! may be the collection described).

Dennstaedtia cornuta (Kaulf.) Mett. Ann. Sci. Nat. V, 2: 260. 1864.

Leaf ca. 2-3 m. long, lamina deltoid, tripinnate to quadripinnate; lower pinnae usually subsessile, with the basal pinnules reduced, apical segments of the pinna separate or nearly so to the prolonged tip, the separate ones closest to the tip obtuse, axes of the penultimate segments without perpendicular herbaceous wings on the upper surface, or with them but the wing on the basiscopic side not decurrent onto the axis of the next order, sterile vein-tips, on the upper surface, clavate to punctate, ending well back of the glabrous margin, pinnules glabrate to usually pubescent beneath, especially on the axes, the brownish trichomes subappressed, ascending, more or less curled; mature indusia purse-shaped to cup-shaped, mostly 1.0-1.5 mm. broad and about half as thick, at least the basal acroscopic ones on an ultimate segment so.

The Swartz material at S-PA consists of two sheets of sterile specimens and one sheet of two fertile specimens. The latter has been appropriately marked "type" by Maxon; only a few of the sori on these specimens are as broad as in typical *D. dissecta*.

This species and the next, *D. obtusifolia*, are very closely related. The only differences that I have been able to find to distinguish them are those of the size and shape of the indusia mentioned in the key. It is quite possible that the two represent a single species with variable sori, but the evidence for this is not conclusive.

Mexico to Panama; Jamaica and Hispaniola; Trinidad to Colombia, south to Bolivia and southern Brazil.

In forests, Huánuco and Junín, 1300-1700 m.

Specimens seen: HUANUCO: Cushi, *Macbride 4844* (F, US); 12 km. w. of Puente Durand, *Stork & Horton 9862* (F, UC); Puente Durand to Exito, *Mexia 8248* (F, GH, UC, US). JUNIN: Schunke Hacienda, above San Ramón, *Killip & Smith 24546* (US); Pichis Trail, San Nicholás, *Killip & Smith 26017* (US).

6. **Dennstaedtia obtusifolia** (Willd.) Moore, Ind. Fil. 306. 1861. FIG. 6.

Dicksonia obtusifolia Willd. Sp. Pl. 5: 483. 1810. Type: Caracas, Venezuela, *Bredemeyer*, Herb. Willd. 20163, B! photo GH, US, fragment LE!

Dicksonia ordinata Kaulf. Enum. Fil. 226. 1824. Type: Porto Rico, *Ventenat* (Kze. Farnkr. t. 106b is evidently drawn from the holotype).

Dicksonia erosa Kze. Linnaea 9: 88. 1834. Type: Pampayacu, Peru, July, 1829, *Poeppig*, presumably destroyed at LZ, fragment (ex Kze.) K!; *Poeppig 169* (det. Kze.) B! photo GH, may augment the fragment at K as authentic material. Authentic specimens are also at P! and LE!

Dennstaedtia ordinata (Kaulf.) Moore, Ind. Fil. 306. 1861.

Dennstaedtia erosa (Kze.) Moore, Ind. Fil. 306. 1861.

Dennstaedtia Orbignyana Kuhn, Linnaea 36: 146. 1869; Chaetopt. 384. 1882. Type: Bolivia, *D'Orbigny 278* B!, photo GH; isotype: P!

Leaf ca. 2-3 m. long, lamina deltoid, bipinnate-pinnatifid to tripinnate, rarely to quadripinnate; lower pinnae usually subsessile, with the basal pinnules reduced, apical segments of the pinna separate or nearly so to the prolonged apex, the separate ones closest to the tip obtuse, axes of the penultimate segments without perpendicular herbaceous wings on the upper surface, or with them but the wing on the basiscopic side not decurrent onto the axis of the next order, sterile vein-tips, on the upper surface, clavate to punctate (rarely slender), ending well back of the glabrous margin; pinnules glabrate to usually pubescent beneath, especially on the axes, the trichomes brownish, subappressed, ascending, more or less curled; mature indusia cup-shaped, mostly 0.5-1.0 mm. broad and about as thick.

This species is closely related to the previous one, *D. dis-*

secta, and the few differences between them are discussed under that species.

Guatemala to Panama; Greater and Lesser Antilles; Trinidad to Colombia, south to Bolivia, Paraguay and southern Brazil.

In forests, San Martín to Ayacucho, 500-1700 m.

Specimens seen: SAN MARTIN: near Tarapoto, *Spruce 4246* (GH, K), *4346* (BM, K). HUANUCO: Pampayacu, *Kanehira 160* (US); Pampayacu, 1829, *Poeppig* (K). JUNIN: Pichis Trail, *Killip & Smith 25550* (US); above San Ramón, *Killip & Smith 24554* (F, US), *Schunke A230* (US); near La Merced, *Killip & Smith 23915* (BM, F, US), *24083* (US); Colonia Perené, *Killip & Smith 24916* (BM, F, US); La Merced, *Soukup 1024* (F); Chanchamayo valley, *Schunke 154* (F, US), *506*, *971* (F). AYACUCHO: Estrella, between Huanta and Río Apurímac, *Killip & Smith 22647* (F, GH, US).

7. **Dennstaedtia arborescens** (Willd.) Maxon, Proc. Biol. Soc. Wash. 43: 88. 1930. FIG. 7.

Davallia arborescens Willd. Sp. Pl. 5: 470. 1810. Type: Santo Domingo, Plumier, Fil. t. 6.

Davallia concinna Presl, Rel. Haenk. 1: 66. 1825, not Schrad. 1818. Syntypes: "Chile, 1790," *Haenke*, 2 sheets PR, photos GH, US. The species is not known from Chile; Presl was undoubtedly correct in later (Epim. Bot. reprint, 102) citing the Haenke collection from Peru.

Dicksonia Pavonii Hook. Sp. Fil. 1: 74. 1844. Based on *Davallia arborescens* Willd., not *Dicksonia arborescens* L'Hérit. (The specimen cited is *Dennstaedtia Sprucei*).

Deparia Mathewsii Hook. Sp. Fil. 1: 85, t. 30B. 1844. Type: Peru, *Mathews 1782* K! fragment P! US!, photo US; isotypes: BM! US!

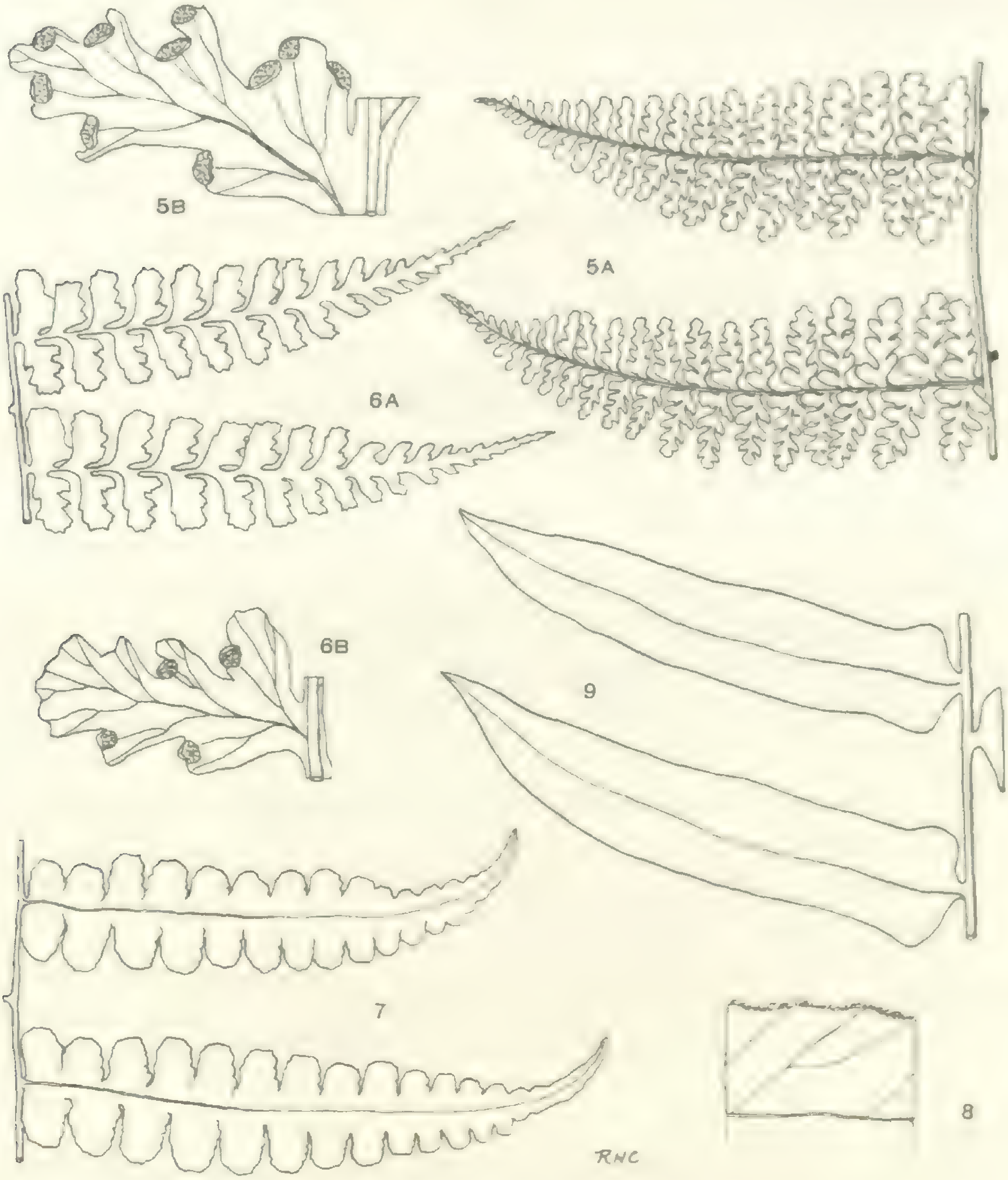
Dennstaedtia concinna (Presl) Moore, Ind. Fil. xcvii. 1857.

Dennstaedtia Pavonii (Hook.) Moore, Ind. Fil. 307. 1861.

Dennstaedtia Mathewsii (Hook.) C. Chr. Ind. Fil. 218. 1905.

Leaf ca. 1.5-3 m. long, lamina evidently ovate, bipinnate to tripinnate; lower pinnae usually subsessile, with the basal pinnules reduced, apical segments of the pinna confluent back of the prolonged tip, the separate ones closest to the tip acute, axes of the penultimate segments without perpendicular herbaceous wings, on the upper surface, or with them but the wing on the basiscopic side not decurrent onto the axis of the next order, sterile vein-tips clavate to punctate, ending well back of the glabrous margin; pinnules glabrate to usually pubescent beneath, the trichomes brownish, subappressed, ascending, more or less curled; mature indusia purse-shaped to usually cup-shaped.

The shape and size of the ultimate segments are quite variable in this species and, in its aspect, the lamina may resemble that of *D. obtusifolia*, or *D. Sprucei*. *Dennstaedtia* *arborescens* and the two previous species, *D. dissecta* and *D. obtusifolia*, sometimes have proliferous buds in the axils of the pinnae; they are evidently more common in this species and rather rare in the other two. These buds are easily detached and presumably can produce young plants when they fall to the ground. I have not, however, seen any material that would substantiate this conclusion.



FIGS. 5-9. Fig. 5. *Dennstaedtia dissecta:* A, pinnules, × ½, Haiti, *Leonard 4740*, GH; B, fertile tertiary segment, × 4, Guatemala, *Türckheim 8629*, GH. Fig. 6. *D. obtusifolia:* A, pinnules, × ¾, Panama, *Killip 12141*, GH; B, fertile tertiary segment, × 4, Porto Rico, *Scamman 6524*, GH. Fig. 7. *D. arborescens:* pinnules, × ½, Haiti, *Ekman H7683*, GH. Fig. 8. *D. Sprucei:* margin of segment, × 10, Peru, *Killip & Smith 25848*, GH. Fig. 9. *D. Wercklei:* pinnae, × ½, Colombia, *Dryander 2446*, GH.

Mexico to Panama; Greater Antilles; Venezuela to Colombia, south to Bolivia.

In forests, San Martín to Puno, 1400-1700 m.

Specimens seen: *Mathews 1782* (BM, K, P, US). SAN MARTIN: near Tarapoto, *Spruce 4346* (BM, GH), *4692* (K); Japalacio, *Stübel 1110* (B). HUANUCO: Huacachi, near Muña, *Macbride 4176* (F, US); Cushi, *Macbride 4842* (F, US). JUNIN: above San Ramón, *Killip & Smith 24642* (F, GH, US); Chanchamayo valley, *Schunke 34, 104* (F). CUZCO: Amaibamba, prov. Convención, *Vargas 9805* (UC); Valle de Occobamba, *Bües 868* (US); Río Arasoa, ne. of Cuzco, *Sandeman 3689* (K); Chaquelloccauca, prov. Convención, *Vargas 12939* (GH). PUNO: San Gabán (Río), *Lechler 2157* (L, B).

8. **Dennstaedtia Sprucei** Moore, Ind. Fil. 308. 1861. Type: Ecuador, *Spruce 5350* (Herb. Hooker), K!; isotype: GH! P!, photo and fragment ex C, US! FIG. 8.

Leaf ca. 1-2 m. long, lamina (shape uncertain) pinnate-pinnatifid to bipinnate-pinnatifid; lower pinnae sessile or subsessile, with the basal pinnules reduced, axes of the penultimate segments without herbaceous wings, on the upper surface, sterile vein-tips clavate to punctate, nearly reaching the persistently pubescent margin; pinnae and pinnules pubescent beneath, especially on the axes, the trichomes brownish, curled; mature indusia purse-shaped to cup-shaped.

Dennstaedtia Sprucei is evidently a rare species and adequate material has not been available to determine the shape of the lamina. The shape and size of the ultimate segments are quite variable and they parallel the similar variation in *D. arborescens*. The persistently pubescent margin, with the vein ends nearly extending to it, are distinctive characters of *D. Sprucei*.

Ecuador and Peru.

Dense forest, Junín, 1700-1900 m.

Specimens seen: "Perou" (F no. 809472). JUNIN: Oxapampa, *Soukup 1826* (GH, US); Dos de Mayo, *Killip & Smith 25848* (BM, GH, US).

9. **Dennstaedtia Wercklei** (Christ) Tryon, Contrib. Gray Herb. 187: 50. 1960. FIG. 9.

Saccoloma Wercklei Christ, Bull. Boiss. II, 4: 1100. 1904. Type: Costa Rica, *Wercklé 320*, P!, photo and figs. in Amer. Fern Jour. 48: pl. 13, 14. 1958.

Dennstaedtia arcuata Maxon, Amer. Fern Jour. 35: 22. 1945. Type: Colombia, *Killip 5565*, US!; isotype: GH!

Microlepia Wercklei (Christ) Kramer, Amer. Fern Jour. 48: 116. 1958.

Leaf ca. 0.5-1.5 m. long, lamina lanceolate, 1-pinnate, pinnae entire, sometimes subauriculate, subsessile, sterile vein-tips clavate to punctate, ending near the glabrous margin; pinnae slightly pubescent beneath, especially on the costa, the trichomes brownish, subappressed, ascending, more or less curled; mature indusia purse-shaped, contiguous and often joined.

The once-pinnate lamina makes this a very distinctive species.

Costa Rica, Colombia and Peru.

In forest, Huánuco, 2000 m.

Specimen seen: HUANUCO: Pozuzo, *Bryan 674* (US).

2. MICROLEPIA Presl, Tent. Pterid. 124. 1836. Type. *Polypodium speluncae* L. = *Microlepia speluncae* (L.) Moore.

Terrestrial, the rhizome long-creeping, pubescent, bearing leaves at intervals; leaves large, tripinnate to quadripinnate, softly pubescent, veins free; sorus roundish, not paraphysate, borne on a vein-tip back from the margin, indusium fully attached to the leaf-tissue along its sides (or in *M. jamaicensis*, the sides partially free), half cup-shaped, the leaf-tissue beyond the sorus not modified. — 2 species in America.

Microlepia speluncae (also in the Old World) is evidently rare and sporadic in its distribution through South America and the West Indies. It has not been collected in Peru but is known from Bolivia. It will probably eventually be found in Peru in forest or ravines of the eastern Andes or adjacent Amazon region. The other American species, *M. jamaicensis*, is confined to the Greater Antilles.

Microlepia speluncae (L.) Moore, Ind. Fil. xciii. 1857.

Rhizome trichomes rather soft, several cells long, these mostly alternately flattened (catenate), the side walls colorless, transparent, the end walls brownish, rather opaque; leaves ca. 0.5-1.5 m. long, long-petioled, lamina lanceolate to broadly lanceolate, pinnae broadest at or near the base, acuminate, softly pubescent beneath and less so above; indusium pubescent.

The indusium and sorus of *Microlepia speluncae* are similar to those of *Saccoloma inaequale*. The two species may be readily separated by the creeping, pubescent rhizome and the pubescent lamina and indusium of *M. speluncae* and the erect, scaly rhizome and the glabrous lamina and indusium of *S. inaequale*. The general aspect of the lamina and the indument of *Microlepia speluncae* are similar to those of *Dennstaedtia cicutaria.* These species may be distinguished by the sorus, which is borne back of the unmodified margin in *M. speluncae* and is marginal and united with the modified margin in *D. cicutaria.*

3. SACCOLOMA Kaulf. Berl. Jahrb. Pharm. 1820: 51. Type: *Saccoloma elegans* Kaulf.

Orthiopteris Copel. Bishop Mus. Bull. 59: 14. 1929. Type: *Davallia ferulacea* Moore = *Orthiopteris ferulacea* (Moore) Copel. (the species has not been placed in *Saccoloma*).

Ithycaulon of auths., including Copel. Univ. Cal. Publ. Bot. 16: 79. 1929. Type: *Davallia moluccana* Bl. = *Tapeinidium moluccanum* (Bl.) C. Chr. This generic name has been erroneously applied to species of *Saccoloma.*

Terrestrial, the rhizome erect, or decumbent with age, scaly, especially at the apex, bearing the leaves in a crown or cluster; leaves of medium size to large, 1-pinnate to tripinnate-pinnatifid, glabrous or nearly so, veins free; sorus borne on a vein tip, not paraphysate, mar-

MAPS 1-2. Map 1, *Dennstaedtia cicutaria.* Map 2, *Saccoloma inaequale.*

ginal (in *S. elegans*) and the indusium narrowly lunate, the pinna margin usually modified, or borne back of the margin (in *S. inaequale*) and the indusium half-conical, attached along its sides, the leaf-tissue beyond not or very slightly modified. — 3 American species.

Tryon, R. The genus Saccoloma Kaulf, *in* Tax. Fern Notes, III. Contrib. Gray Herb. 191: 100-106. 1962.

KEY TO SPECIES

a. Lamina bipinnate or more complex. .... b.
  b. Lamina rather finely cut into mostly small, strongly toothed or lobed ultimate segments, its apex cut almost to the rachis; sori distant, indusium narrowly cuneate, shorter than the unmodified, opposed margin. .... 1. *S. inaequale*
  b. Lamina coarsely cut into mostly large, entire to shallowly toothed ultimate segments, its apex pinnatifid; sori mostly on adjacent vein-ends, indusium broadly cuneate, nearly equal to the short, somewhat modified, indusiform marginal lobule; West Indies, Venezuela, Colombia, Brazil. ...... *S. domingense* (Spreng.) C. Chr.
a. Lamina 1-pinnate, the pinnae simple. .... 2. *S. elegans*

1. **Saccoloma inaequale** (Kze.) Mett. Ann. Sci. Nat. IV, 15: 80. 1861. FIG. 10, MAP 2.

Davallia inaequalis Kze. Linnaea 9: 87. 1834. Type: Yurimaguas, Maynas, (now Alto Amazonas, Loreto), Peru, Dec. 1830, *Poeppig, Diar. 2113*, probably destroyed at LZ; isotype: B! photo GH, GH!

Saccoloma inaequale var. *caudata* Hieron. Hedwigia, 47: 207. 1908. Type: near Yquitos and Cocha (in the Marañon valley), Peru, *Stübel 1129*, B.

Orthiopteris inaequalis (Kze.) Copel. Gen. Fil. 50. 1947.

Rhizome quite erect; leaf ca. 1 m. (-1.5 m.) long, long-petioled, lamina bipinnate to quadripinnate, deltoid to long-triangular, rather finely cut into mostly small, strongly toothed or lobed ultimate segments, the apex gradually reduced, cut almost to the rachis, long-triangular, veins more or less evident beneath; sori distant, indusium glabrous.

There is considerable variation in the size of the ultimate segments, the degree to which they are lobed and the form of the apex of the penultimate segments. None of the variations appears to merit taxonomic recognition.

Mexico and Central America; West Indies; Guianas to Colombia, south to Bolivia; Brazil.

In woods and dense forest, Loreto and San Martín to Puno, 100-1700 m.

Selected specimens: SAN MARTIN: Tarapoto, *Spruce 4691* (K), *L. Williams 6007* (F, GH); Cumbassauma Mts. (near Tarapoto), *Steere* (GH); Rioja, *Stübel 1056* (B). LORETO: Iquitos, *Ule 6884* (K), *Killip & Smith 30687, 37319* (F, US); Tierra Doble, alto Río Nanay, *L. Williams 1053* (F); Mishuyacu, near Iquitos, *Klug 239* (F, US); Yurimaguas, Maynas, *Poeppig* (K), *2113* (B, GH); Yurimaguas, *L. Williams 4421* (F, GH), *Killip & Smith 28033* (US). HUANUCO: Tingo María, *Asplund 12242* (K, US), *Ferreyra 10320* (GH, USM), *Tryon & Tryon 5223* (BM, F, GH, U, US, USM); 5 km. ne. of Tingo María, *Stork & Horton 9524* (F, UC); 30 km. n. of Tingo María, *Stork & Horton 9483* (F, UC). JUNIN: Yapas, Pichis Trail, *Killip & Smith 25548* (US); Schunke Hacienda, above San Ramón, *Schunke A232* (GH, US); near La Merced, *Killip & Smith 23988* (F, GH, US); Puerto Bermudez, *Killip & Smith 26468* (F, US); Puerto Yessup, *Killip & Smith 26368* (F, US). PUNO: San Gabán (Río), *Lechler 2293* (B, photo GH, K); Chunchusmayo, Sandia, *Weberbauer 1263* (B, photo GH).

2. **Saccoloma elegans** Kaulf. Berl. Jahrb. Pharm. 1820: 51. Type: None cited, but in Enum. Fil. 224, t. 1, 1824, Kaulfuss cites *Sello*, Brazil, which may be accepted as the type; a specimen at B! photo GH, is undoubtedly an isotype. FIG. 11.

Rhizome erect to decumbent with age; leaf ca. 1-1.5 m. long, long-petioled, lamina 1-pinnate, ovate-oblong, apex with a conform terminal pinna, pinnae simple, long-elliptical to oblong-elliptical, crenulate to dentate at the acuminate apex, veins prominent beneath; sori very numerous along the margin, contiguous, indusium glabrous.

Central America; Greater Antilles; Trinidad and the Guianas to Colombia, south to Bolivia; Brazil.

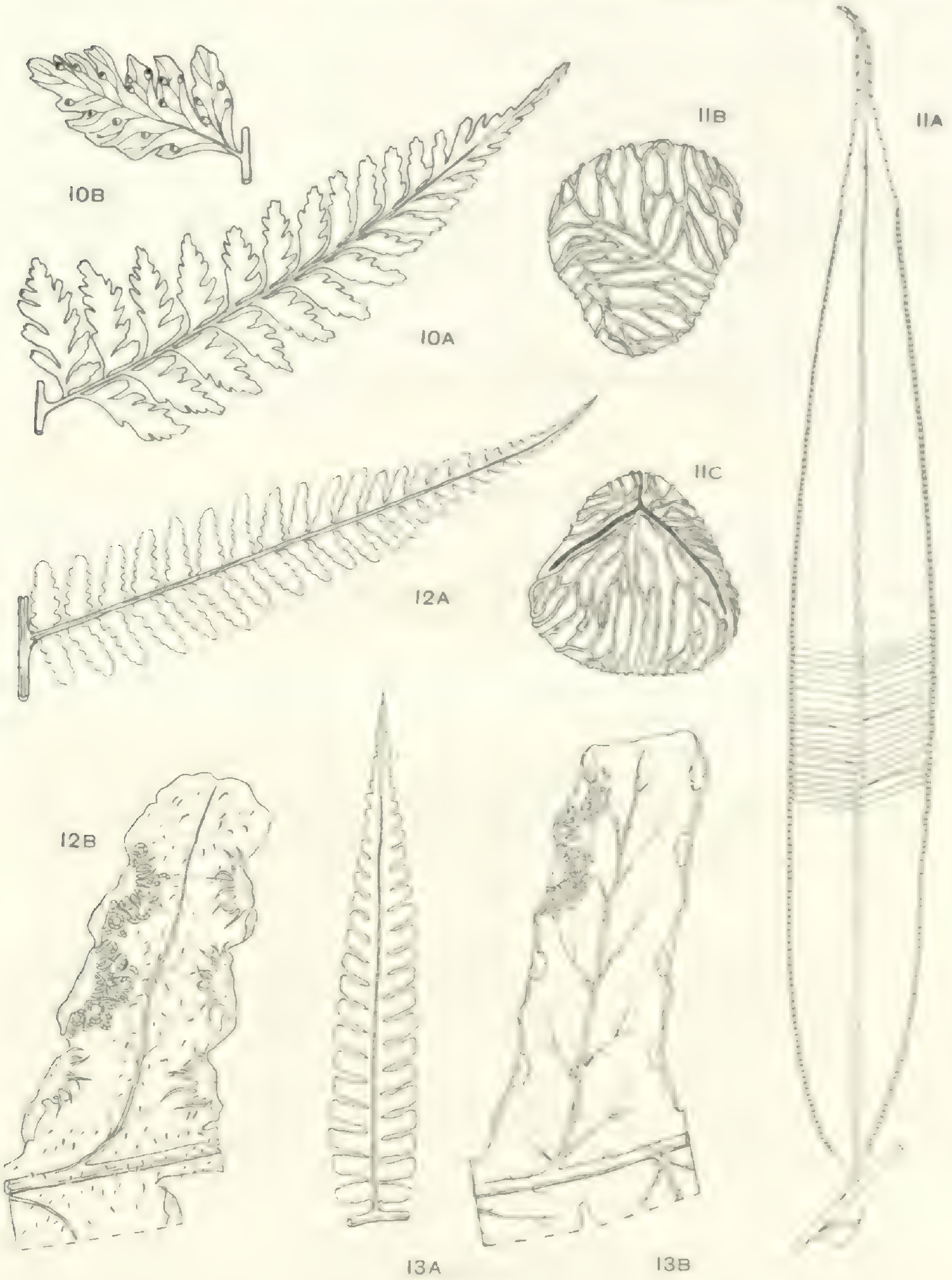
In woods and dense forest, Loreto, Junín and Puno, 100-1700 m.

Specimens seen: LORETO: Iquitos, *Killip & Smith 27121* (F, NY, US). JUNIN: San Nicolás, Pichis Trail, *Killip & Smith 26072* (F, GH, NY, US); Schunke Hacienda, above San Ramón, *Killip & Smith 24574* (GH, NY, US), *Schunke A231* (GH, US); La Merced, *Soukup 1090* (F). PUNO: San Gabán (Río), *Lechler 2416* (B).

4. HYPOLEPIS Bernh. Neues Jour. Bot. Schrad. 1(2):34. 1805. (1806). Type: *Lonchitis tenuifolia* Forst. = *Hypolepis tenuifolia* (Forst.) Bernh.

Terrestrial, the rhizome slender, long-creeping, pubescent, bearing the leaves at intervals; leaves of medium size to very large, bipinnate-pinnatifid to quadripinnate-pinnatifid, glabrate to usually pubescent, veins free; sorus borne on a vein-tip ending at a sinus, not paraphysate, the sporangia more or less covered by the indusium which is formed from a reflexed, more or less modified, marginal lobe. — About 20 species in America.

Some of the species, especially *Hypolepis hostilis*, are similar to *Pteridium* in their ecology and manner of growth;



FIGS. 10-13. Fig. 10. ***Saccoloma inaequale:*** A, pinnule, × ½, Peru, ***L. Williams 4421***, GH; B, fertile tertiary segment, × 1, ***idem.*** Fig. 11. ***S. elegans:*** A, fertile pinna, × ½, Panama, ***Killip 2531***, GH; B, basal view of spore, enlarged, Ecuador, ***Mexia 8429***, GH; C, apical view of spore, enlarged, ***idem.*** Fig. 12. ***Hypolepis Stuebelii:*** A, pinnule, × ¾, Colombia, ***Killip & Smith 19368***, GH; B, fertile tertiary segment, × 7, ***idem.*** Fig. 13. ***H. parallelogramma:*** A, pinnule, × ½, Peru, ***Mexia 8149***, GH; B, fertile tertiary segment, × 5, ***idem.***

the two may grow together in recently cleared areas. However, the species of *Hypolepis* never become pernicious weeds as *Pteridium* sometimes does. The usually large leaves are not well represented as herbarium specimens, nor are the rhizomes or juvenile plants. The latter may have (see *H. hostilis*) a different type of indument than the adult leaf. It is anticipated that better and more representative collections will lead to an improved classification of the American species. *Hypolepis viscosa* Karst. of Colombia may possibly be discovered in Peru. It is similar to *H. Stuebelii* in its ciliate indusium. However, the lamina is glandular-pubescent beneath (lacking the long stiff trichomes of *H. Stuebelii*) and it has numerous short, glandular trichomes on the upper surface.

KEY TO SPECIES

a. Indusium long-ciliate with few-celled trichomes; lower surface of the segments with moderately long, straight or curved, few-celled, terete, stiff, pointed trichomes (shorter, gland-tipped ones may also be present); stipe, rachis and pinna-rachises aculeolate or very sparingly so. .... 1. *H. Stuebelii*

a. Indusium glabrous, smooth on the edge to erose-fimbriate; lower surface of the segments glabrous or with multicellular, often moniliform, or gland-tipped trichomes. .... b.

  b. Ultimate segments, or many of them, squarish or very bluntly obtuse; lower surface of the segments glabrous or very slightly pubescent; rachis and pinna-rachises aculeolate, especially beneath. .... 2. *H. parallelogramma*

  b. Ultimate segments rounded at the apex. .... c.

    c. Lower surface of the segments with multicellular, often long, tortuous and moniliform trichomes with a pointed apex, these sometimes forming a tomentum. .... d.

      d. Rachis flexuous, subdichotomous toward the base; lower pinnae much larger than those above, strongly inequilateral. .... 3. *H. bogotensis*

      d. Rachis quite or nearly straight, lower pinnae not much, if at all, larger than those above, nearly or quite equilateral. .... 4. *H. obtusata*

    c. Lower surface of the segments very slightly to rather densely pubescent, the trichomes various but some gland-tipped or clavate-tipped; rachis and usually the pinna-rachises aculeolate. .... 5. *H. hostilis*

1. **Hypolepis Stuebelii** Hieron. Hedwigia 48: 230, t. 10, fig. 8. 1909. Type: near San Florencio, prov. Manabí, Ecuador, *Stübel 796*, B! fragment US!; isotype: GH! FIG. 12.

Leaf to 1 m. (or more) tall, more or less erect; lamina tripinnate-pinnatifid to quadripinnate, rachis straight, it and the pinna-rachises aculeolate or sparingly so, lower pinnae larger than those above, inequilateral; segments pubescent beneath with moderately long, straight or curved, stiff, few-celled, terete, pointed trichomes, a few shorter gland-tipped ones may also be present, ultimate segments broadly rounded to subacute; indusium long-ciliate.

The long-ciliate indusium as well as the distinctive pubescence on the lower surface of the segments amply distinguish this species. The related *Hypolepis rigescens* (Kze.) Moore has similar indument but a non-ciliate indusium.

Greater Antilles; Venezuela to Colombia, south to Peru.

In pastures, rocky open places and rocky woods, Junín and Cuzco, 1450-2300 m.

Specimens seen: JUNIN: Chanchamayo valley, *Schunke 689* (F), *942* (F, US). CUZCO: Cerro de Cusilluyoc, *Pennell 14025* (F, GH); Choquellouanca, prov. Convención, *Vargas 12936* (GH).

2. **Hypolepis parallelogramma** (Kze.) Presl. Tent. Pterid. 162. 1836. FIG. 13.

Cheilanthes parallelogramma Kze. Linnaea 9: 85. 1834. Type: Pampayacu, Peru, July, 1829, *Poeppig*. Hb. Kze. presumably destroyed at LZ; fragment ex Kze., LE! photo GH.

Leaf to 3-3.5 m. (to 7 m.) long, scandent, lamina tripinnate to tripinnate-pinnatifid, rachis more or less straight, it and the pinna-rachises aculeolate, lower pinnae not much if any larger than those above, nearly equilateral; segments glabrous beneath or sometimes very slightly pubescent with multicellular, sometimes long, tortuous and moniliform trichomes with a pointed or rarely gland-tipped apex, ultimate segments squarish or very bluntly obtuse, or many of them so; indusium glabrous, smooth on the edge.

The exceptionally long leaf is reported to be scandent over shrubs, or the apical portion pendant from the lower branches of trees. The shape of the ultimate segments and the usually glabrous segments serve to distinguish specimens of this species. In some portions of the lamina the ultimate segments are three times as long as broad with parallel and entire margins, and they present a distinctive type of leaf-cutting. However, in other portions, they may be strongly crenate or lobed and are often broader at the base.

Venezuela to Colombia, south to Bolivia; Brazil.

In forests, Huánuco, Junín and Cuzco, 1500-1800 m.

Specimens seen: HUANUCO: Pampayacu, *Poeppig* (LE); Puente Durand to Exito, *Mexia 8149* (BM, F, GH, MO, UC, US). JUNIN: Chanchamayo valley, *Schunke 83* (F, US), *508* (F); San Ramón, *Schunke A182* (GH,US); Eneñas, Pichis Trial, *Killip & Smith 25760* (F, GH, US). CUZCO: Valle San Miguel, prov. Convención, *Bües 2086, 2092* (US); Quince Mil, *Vargas 10096* (UC).

3. **Hypolepis bogotensis** Karst. Fl. Columb. 2: 91, t. 147. 1865. Type: "Cordillerae Bogotensis, 2900-3000 m.", *Karsten*, LE! photo GH; isotype: B! FIG. 14.

Hypolepis flexuosa Sod. Crypt. Vasc. Quit. 634. 1893. Type: "Volcán el Corazón, 2900 m.", Ecuador, *Sodiro*, P! photo GH.

Leaf to 2 m. (or more ?) tall, lamina to quadripinnate-pinnatifid or quinquepinnate-pinnatifid, rachis flexuous, subdichotomous toward the base, it and the pinna-rachises not aculeolate, lower pinnae much larger than those above, strongly inequilateral; segments densely tomentose to slightly pubescent beneath with multicellular, usually long and tortuous, moniliform, pointed trichomes, these shorter and straighter when the segment is slightly pubescent, ultimate segments rounded to narrowly rounded at the apex; indusium slightly to moderately and irregularly erose-fimbriate.

The flexuous rachis which is subdichotomous toward the base and the large inequilateral lower pinnae are the most distinctive characters of this species. The penultimate segments are often rather long stalked and triangular.

Costa Rica; Venezuela to Colombia, south to Bolivia.

At edge of woods and in dense jungle, San Martín and Huánuco, 3500-3700 m.

Specimens seen: SAN MARTIN: Bagazan, *Stübel 1071* (B). HUANUCO: Tambo de Vaca, *Macbride 4381* (F, US); 15 miles ne. of Huánuco, *Macbride & Featherstone 2199* (F, NY, US).

4. **Hypolepis obtusata** (Presl) Hieron. Hedwigia 48: 228. 1909. (Kuhn, Chaetopt. 347. 1882, not a proper transfer). FIG. 15.

Cheilanthes obtusata Presl, Rel. Haenk. 1: 64: t. 11, fig. 1. 1825. Type: Mountains of Peru, *Haenke*, PR.

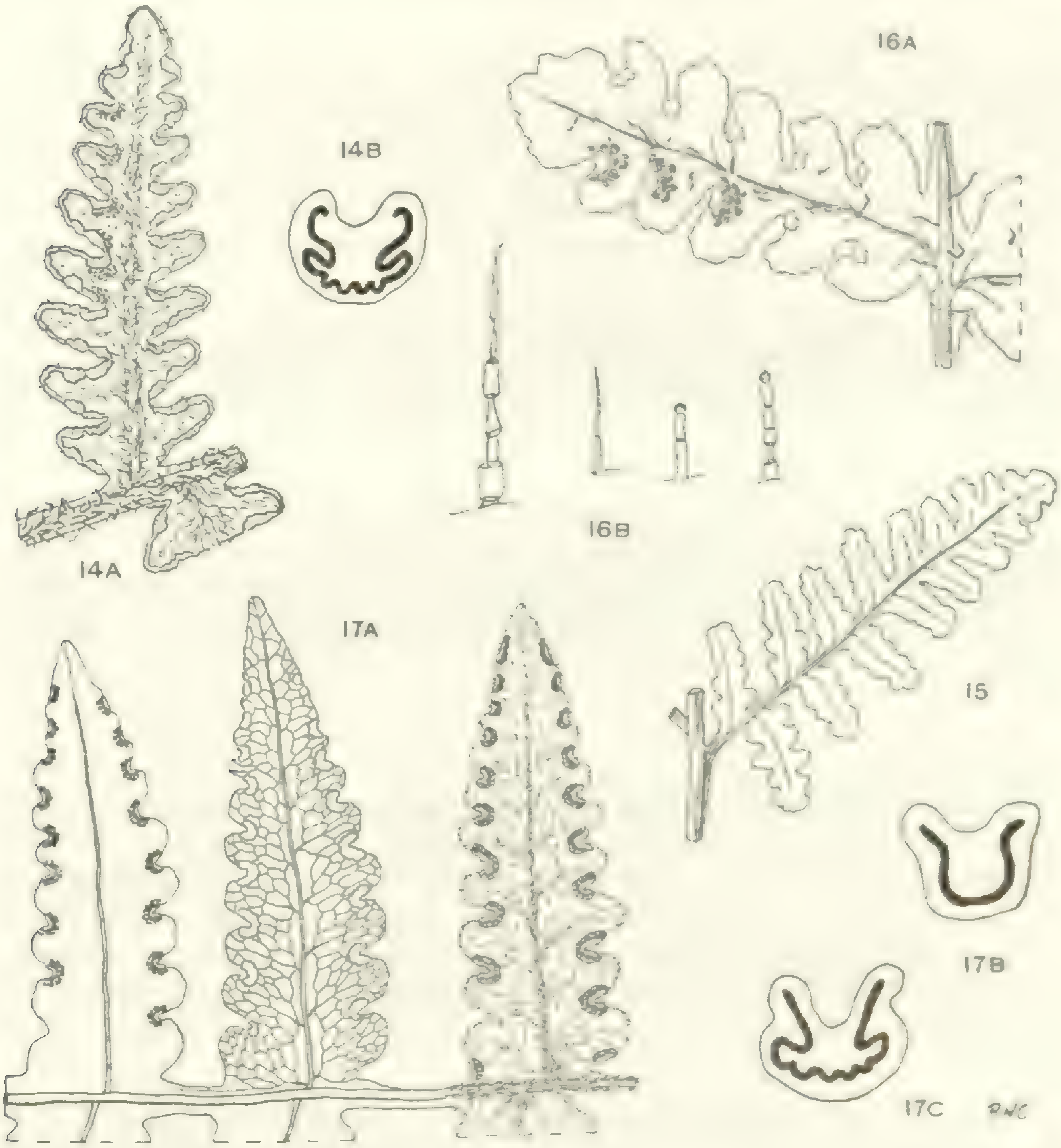
Polypodium fulvescens Hook. & Grev. Hook. Bot. Misc. 2: 239. 1831. Type: Huaylluay (Hucayllay), near Pasco, Peru, *A. Cruckshanks*, K, photo and fragment US!; isotype: GH!

Plecosorus peruvianus Fée. Gen. Fil. 151. 1852. Type: Peru, *Pavon*; isotype: K! photo GH, US.

Hypolepis pteroides Mett. Fil. Lechl. 1: 17, t. 3, figs. 7-13. 1856. Type: St. Gavan, (Río San Gaban) Peru, *Lechler 2152*, B! photo GH, fragment US!; isotype: K! photos GH, US, fragment US!

Leaf ca. 0.08-1.0 m. tall, erect, lamina bipinnate-pinnatifid to tripinnate-pinnatifid, rachis straight, it and the pinna-rachises not aculeolate, lower pinnae smaller than to slightly larger than those above, nearly or quite equilateral; segments moderately to rather densely pubescent beneath with multicellular, long, tortuous, moniliform, pointed trichomes, ultimate segments rounded at the apex; indusium nearly smooth on the edge to moderately erose-fimbriate.

Hypolepis obtusata is represented by rather few specimens and it is not yet sufficiently known. It is evidently



FIGS: 14-17. Fig. 14 *Hypolepis bogotensis:* A. small fertile pinnule, × 2½, Colombia, *Pennell & Hazen 10086*, GH; B, petiole section, × 2. Colombia, *Tryon & Tryon 6117*, GH. Fig. 15. *H. obtusata:* pinna, × 1, Peru, *Cruckshanks*, GH. Fig. 16. *H. hostilis:* A, fertile tertiary segment, × 5. Bolivia, *Steinbach 9302*, GH; B, types of laminar trichomes, enlarged, *idem*. Fig. 17. *Blotiella Lindeniana:* A, fertile pinnules, × ¾, Colombia, *Kalbreyer 995*, GH; B. petiole section, × 4. Jamaica, *Watt*, NY; C, petiole section, × 2, Brazil, *Brade 9390*, NY.

allied to *H. bogotense* by the similar pubescence and non-aculeate axes. It differs from that species in the characters of the rachis and lower pinnae mentioned in the key. The leaves vary greatly in size, the smaller ones having a proportionately shorter and narrower lamina. *Vargas 6976*, perhaps collected when the leaves were rather young, has the upper surface of the segments shortly glandular-pubescent as in *H. viscosa*.

Colombia to Peru.

Among rocks, Junín, Cuzco and Puno, 2800-3400 m.

Specimens seen: JUNIN: Hucayllay, *Cruckshanks* (GH, US). CUZCO: Ccaocco, *Bües 1399* (US). PUNO: Achopampa, prov. Carabaya, *Vargas 6976* (UC); "Tabina", *Lechler 2094* (B); San Gabán (Río), *Lechler 2152* (B).

5. **Hypolepis hostilis** (Kze.) Presl, Tent. Pterid. 162. 1836. FIG. 16, MAP 3.

Cheilanthes hostilis Kze. Linnaea 9: 86. 1834. Type: Mission Tocache, upper Huallaga, July, August, 1830, Peru, *Poeppig (Diar. 1957)*, Hb. Kze. presumably destroyed at LZ; *Poeppig*, Peru, 1829, K! photo and fragment US! is probably authentic.

Hypolepis parviloba Fée, Crypt. Vasc. Brésil. 1: 53, t. 20, fig. 1, 1869. Type: near San Gabriel da Cachoeira, Río Negro, Brazil, *Spruce 2119*, P! (Herb. Glaziou ex Fée); isotypes: K! GH! US!

Hypolepis Buchtienii Rosenst. Fedde Rep. Spec. Nov. 25: 58. 1928. Type: Hacienda Casana, valle Tipuani, Bolivia, *Buchtien 7014*, S-PA!; isotype: US!

Leaf to ca. 2 m. tall, erect or nearly so, lamina quadripinnate to quadripinnate-pinnatifid, rachis straight, it and usually the pinna-rachises aculeolate, lower pinnae not much, if at all, larger than those above, equilateral or nearly so; segments very slightly to densely pubescent beneath with short, more or less moniliform, straightish or subtortuous, multicellular or few-celled, gland- or clavate-tipped trichomes, or sometimes a few trichomes with pointed tips, ultimate segments rounded to subacute at the apex; indusium nearly smooth on the edge to definitely erose-fimbriate.

The aculeolate rachis and gland- or clavate-tipped trichomes serve to distinguish *Hypolepis hostilis.* The ultimate segments are usually small and somewhat distant so that the leaf-cutting has a more lacy appearance than in the other species. The least pubescent leaves have only a short, glandular pubescence while the most pubescent ones have also a mixture of longer, pointed trichomes. A collection from

Tingo María *(Tryon & Tryon 5240)* shows a different type of leaf indument in juvenile and adult plants. The smallest leaves have only large, broad whitish, pointed, moniliform trichomes. This perhaps is parallel to the situation in *Pteridium aquilinum* in which the pubescence of the juvenile leaves, in some varieties, is different from that in the adult leaves.

Colombia to Bolivia; Brazil.

In dense forest or along forest borders, or in cut-over areas, Loreto and San Martín to Puno, 100-1300 m.

Specimens seen: SAN MARTIN: Divisoria, *Ferreyra 1048* (BM). LORETO: San Lorenzo, between mouths of Río Pastaza and Río Huallaga, *Killip & Smith 29207* (US); Mishuyacu, near Iquitos, *Klug 469, 1389* (F, US). HUANUCO: Tingo María, *Allard 21678* (US), *Tryon & Tryon 5240* (BM, F, GH, U, US, USM). JUNIN: San Ramón, *Schunke A181* (US); Chanchamayo valley, *Schunke 48* (F, US); Carpapata, *G. Kunkel 550* (GH). PUNO: San Gabán (Río), *Lechler 2334* (B).

5. BLOTIELLA Tryon, Contrib. Gray Herb. 191: 96. 1962. Type: *Lonchitis glabra* Bory = *Blotiella glabra* (Bory) Tryon.

Lonchitis of auths., not L.

Terrestrial, the rhizome stout, decumbent (in our species), pubescent, bearing the leaves in a cluster; leaves large, pinnate-pinnatifid to bipinnate-pinnatifid, more or less pubescent, veins anastomosing; sorus marginal, paraphysate, borne in the sinus of segments or small lobes, the sporangia borne on a short vascular commissure, covered by the indusium which is formed from the reflexed, modified margin. — 1 American species.

Kümmerle, J. B. Monographiae generis Lonchitidis prodromus. Bot. Közlem. 1915: 166-188.

Tryon, R. The genera Lonchitis and Blotiella, *in* Tax. Fern Notes, III. Contrib. Gray Herb. 191: 93-100. 1962.

Blotiella Lindeniana (Hook.) Tryon, Contrib. Gray Herb. 191: 99. 1962. FIG. 17.

Lonchitis Lindeniana Hook. Sp. Fil. 2: 56. t. 89A. 1851. Type: Caracas, Venezuela, *Linden 543*, K! photo GH; isotype: BR photo GH, US!

Rhizome trichomes long, of many long cells, these with whitish to brown side walls and brownish cross walls; leaf to 2 m. (or more ?) long, lamina lanceolate in small leaves, ? in large ones, pinnae (with rare exceptions) sessile or short-stalked, the basal pinnules usually reduced, especially on the lower pinnae, pinnules entire to pinnatifid, obtuse to acute, all parts of the lamina more or less pubescent with long, acicular trichomes, which may be gland-tipped, or not; indusium more or less pubescent.

There is a single species of this predominantly African genus in the American tropics. It is evidently rare and local and more adequate collections are needed in order to determine the lamina shape and to understand apparently minor variations in characters of the indument.

Costa Rica; Jamaica and Hispaniola; Venezuela to Colombia, south to Bolivia.

Huánuco.

Specimens seen: HUANUCO: between Huánuco and Pampayacu, *Kanehira 140* (GH, US).

TRIBE 6. CHEILANTHEAE.

6. ERIOSORUS Fée, Gen. Fil. 152, t. 13B, f. 1. 1852. Type: *Eriosorus scandens* Fée = *Eriosorus aureonitens* (Hook.) Copel.

Psilogramme Kuhn, Fest. 50 Jub. Reals. Berl. (Chaetopt.) 332. 1882. Type: *Gymnogramma elongata* Hook. & Grev. = *Eriosorus elongatus* (Hook. & Grev.) Copel.

Terrestrial, the rhizome slender, creeping, pubescent or with bristle-like trichomes, bearing the leaves closely or widely spaced; leaves small to large, pinnate-pinnatifid to quadripinnate-pinnatifid, pubescent or glandular-pubescent, veins free; sporangia borne along a portion of the veins, back of the nearly unmodified margin, indusium and paraphyses absent. — About 30 American species.

The treatment of this genus has been prepared by Alice F. Tryon on the basis of studies preliminary to a revision of the whole genus. *Eriosorus* is principally a genus of the South American Andes from Bolivia to Venezuela. In Peru it typically grows in the moist and cool zone of the eastern slopes of the Andes between 2500 and 3500 m. Some species have a determinate lamina that becomes fully expanded, while others have an indeterminate lamina that retains a coiled bud at the apex.

KEY TO SPECIES

a. Lamina long-deltoid or sublanceolate, some (or all) of the lower pinnae twice as long as those toward the apex. .... b.

b. Leaves erect or subscandent, bi- to tripinnate. .... c.

c. Pinnae sessile or with stalks less than 1 cm. long, rachis straight or nearly so, leaves determinate or the apical bud minute. .... d.

d. Pinnae rigid-herbaceous or chartaceous, vein-ends acute or clavate, both surfaces of the pinnae with abundant, short, capitate, glandular trichomes. .... 1. *E. Lechleri*

d. Pinnae subcoriaceous, vein-ends flabellate, both surfaces of the pinnae with long, acuminate (rarely capitate) trichomes. .... e.

e. Pinnae with rigid, bicolorous trichomes on both surfaces and along the margin. .... 2. *E. rufescens*

e. Pinnae with sericeous, tan trichomes on both surfaces. .... 3. *E. Stuebelii*

c. Basal pinnae petiolulate, the stalks 1-25 cm. long, rachis usually flexuous, leaves with indeterminate growth, the apical buds large. .... f.

f. Lower surface of the pinna visible beneath the tan pubescence, vein-ends terminating at the margin. .... 4. *E. accrescens*

f. Lower surface of the pinna obscured by the rust-colored tomentum, vein-ends protruding as a tooth from the margin. .... 5. *E. aureonitens*

b. Leaves scandent, quadripinnate or more complex. .... g.

g. Ultimate segments dichotomously divided or deeply bifid, usually several times longer than broad, with 1 or 2 veins, pinna-rachises flexuous, the pinnules ascending, or at a right-angle to the pinna-rachis. .... 6. *E. flexuosus*

g. Ultimate segments ovate to flabellate, about as broad as long, with 4-15 veins, pinna-rachises arcuate, the pinnules mostly descending-curved. .... 7. *E. Orbignyanus*

a. Lamina linear-elongate, the pinnae of nearly the same length throughout. .... h.

h. Leaves bipinnate-pinnatifid, the pinnules 1-2 mm. distant, spores usually light amber-colored to light brown, rhizome trichomes with an acuminate apex. .... 8. *E. flabellatus*

h. Leaves pinnate-pinnatifid, rarely bipinnate, the lobes or pinnules imbricate or adjacent, spores dark brown, rhizome trichomes with a bulbous apical cell. .... 9. *E. elongatus*

1. **Eriosorus Lechleri** (Kuhn) A. F. Tryon, Rhodora 65: 56. 1963. FIG. 18.

Gymnogramma Lechleri Kuhn, Linnaea 36: 71. 1869. Type: San Gavan, (Río San Gaban) Puno, Peru, *Lechler 2262*. B! photo GH.

Psilogramme Lechleri (Kuhn) Kuhn, Fests. 50 Jub. Reals. Berol. (Chaetopt.) 339. 1882.

Rhizome not seen; leaves erect, with indeterminate growth, lamina elongate-deltoid or sublanceolate, acuminate, bipinnate-pinnatifid to tripinnate, rachis castaneous, straight or nearly so, pinnae deltoid, or the apical ones ovate and decurrent on the rachis, the basal petiolulate with stalks less than 0.5 mm. long, slightly shorter than the pair above, pinnules deltoid or ovate, rigid-herbaceous, both upper and lower surfaces with some long clear trichomes having acuminate apical cells and abundant short trichomes with the apex bulbous, ultimate lobes bifid or crenulate. Vein branches departing at moderately broad angles, the ends extending to, or nearly to, the margin, acute to clavate; spores dark brown.

Peru.
Cuzco and Puno, 2700 m.

Specimens seen: CUZCO: Los Palmitos, *Bües 1915* (US). PUNO: San Gabán (Río), *Lechler 2262* (B).

2. **Eriosorus rufescens** (Fée) A. F. Tryon, Rhodora 65: 56. 1963. FIG. 19.

Gymnogramma rufescens Fée, Gen. Fil. 181, t. 19C, f. 3. 1852. Type: "Andibus", Peru, *Mathews*.

Gymnogramma mohriaeformis Mett. Fil. Lechl. 1: 9. 1856. Type: San Gavan (Río San Gabán), Puno, Peru, *Lechler 2255*, B! photo GH, fragment NY!

Gymnogramma Mathewsii Hook. Sp. Fil. 5: 128, t. 290. 1864. Type: Peru, *Mathews 1814*, K! photo GH.

Psilogramme rufescens (Fée) Kuhn, Fests. 50 Jub. Reals. Berol (Chaetopt.) 336. 1882.

Psilogramme Mathewsii (Hook.) Kuhn, Fest. 50 Reals. Berol. (Chaetopt.) 336. 1882.

Rhizome long-creeping, dichotomously branching, 2-4 mm. in diam., with rigid, appressed, bristle-like trichomes with 1-5, usually 2, cells at the base, darker than the rhizome surface, the apex acuminate; leaves erect, determinate, lamina elongate-deltoid, acuminate, bipinnate, rachis castaneous, straight, pinnae deltoid to ovate, subsessile or with very short stalks, the apical ones decurrent on the rachis, pinnules subdeltoid or ovate, subcoriaceous, upper and lower surfaces with rigid, clear or bicolorous trichomes, acuminate or rarely with a bulbous apical cell, ultimate segments broadly lobed to crenulate, vein branches moderately acute the vein-ends extending to the margin, flabellate; spores usually light amber colored, rarely dark brown.

This species is distinguished from the others in Peru by the rigid, bicolorous trichomes. There is considerable variation in the size of the leaves and the Lechler collection, which is the type of *Gymnogramma mohriaeformis*, is an unusually small-leaved specimen.

Andean, Venezuela to Bolivia.

On mossy banks, in sphagnum, montaña, Libertad to Cuzco, 2440-3600 m.

FIGS. 18-20. Fig. 18. *Eriosorus Lechleri*: A. architecture of lamina. × ½, Peru, *Lechler 22[illegible]2*, B; B. pinna. × 1, Peru, *[illegible]* [illegible]. Fig. 19. *E. [illegible]*: A. architecture of lamina. × ½, Peru, *[illegible]*, [illegible]; B. pinna. × 1, idem. Fig. 20. *E. accrescens*: A. architecture of lamina. × ½, Peru, *[illegible]*, [illegible]; B. pinna, × 1, idem.

Specimens seen: LIBERTAD: Pumatambo, Puerto del Monte, *López & Sagástegui 3436* (GH). HUANUCO: Cushi, *Bryan 683* (US); Pampayacu, *Kanehira 166* (GH, US); Muña, *Macbride 4302* (F, GH), Playapampa, *Macbride 4513* (F, GH). CUZCO: Huadquiña, *Bües 972* (US); La Convención, *Bües 2142* (US); Prov. Urubamba, *Vargas 2897* (US); Paucartambo, *Vargas 12192* (GH).

3. **Eriosorus Stuebelii** (Hieron.) A. F. Tryon, Rhodora 65: 57. 1963.

Gymnogramma Stuebelii Hieron. Hedwigia 48: 219, t. 9, f. 5. 1909. Type: Mojon-Cruz, inter Pacasmayo et Moyobamba, Peru, *Stübel 1058,* B! photo and fragment GH!

Rhizome not seen; leaves erect, determinate, lamina elongate-deltoid, acuminate, bipinnate, rachis straight, pinnae deltoid to ovate, the apical ones decurrent, the basal ones with very short stalks, nearly subsessile, pinnules ovate, subcoriaceous, upper and lower surfaces with tan, sericeous tomentum, the trichomes with acuminate apex, ultimate segments crenulate, vein branches moderately broad, the vein-ends flabellate, terminating in a sinus at the margin; spores dark brown (irregular or shriveled).

This species is known only from the original collection from northern Peru. The region between Pacasmayo and Moyobamba has been little collected since Stübel made his trip across the Andes.

Eriosorus Stuebelii most closely resembles *E. rufescens* in the determinate leaves and the deltoid, nearly sessile, pinnae. The tan, sericeous tomentum, particularly on the upper pinna surface, of *E. Stuebelii,* however, is quite distinct from the rigid, bicolorous trichomes on the pinnae of *E. rufescens.*

Peru.

Specimen seen: Mojon-Cruz inter Pacasmayo et Moyobamba, 3300 m., *Stübel 1058* (B).

4. **Eriosorus accrescens** A. F. Tryon, Rhodora 65: 57, 1963. FIG. 20.

Type: Puyupata to "Yuncapata", Prov. Urubamba, Peru, *Vargas 2921* US!

Rhizome not seen; leaves subscandent or pendent, with indeterminate growth, lamina elongate-lanceolate or elongate-ovate, bipinnate-pinnatifid or tripinnate, rachis castaneous becoming lighter colored toward the apex, somewhat flexuous, pinnae deltoid, petiolulate, the stalks ca. 1.0 cm. long, pinnules deltoid or ovate, subcoriaceous, upper and lower surfaces with tan, sericeous pubescence, somewhat denser on the lower surface along the veins, the trichomes with acuminate apex, ultimate segments bluntly lobed to crenulate, vein branches departing at moderately broad angles, the vein-ends flabellate, terminating in a sinus at the margin; spores dark brown.

In the habit and form of the leaves, in the stalked pinnae and the sericeous indument on the pinnae this species most closely resembles *E. aureonitens.* The indument is tan and less dense in *E. accrescens* and the vein-ends terminate at the margin, while in *E. aureonitens* the lamina is covered by a rust-colored tomentum and the veins protrude in a tooth from the margin.

Peru.

Wooded ravine, Amazonas and Cuzco, 2950-3350 m.

Specimens seen: AMAZONAS: entre Leimebamba y Balsas, *López et al. 4444* (GH). CUZCO: Huadquiña, *Bües 992* (US); Valle de Lares, Montaña de Colca, *Bües 1925* (US); Altura de Chaco, *Bües 2135* (US).

5. **Eriosorus aureonitens** (Hook.) Copel. Gen. Fil. 58. 1947. FIG. 21.

Gymnogramma aureonitens Hook. Icon. Pl. 9: t. 820. 1852 (prior to May, cf. Gard. Chron. 1852: 278). Type: Peru, *W. Lobb,* K! photo GH, fragment NY!

Eriosorus scandens Fée, Gen. Fil. 152, t. 13B, f. 1. 1852 ("probably December," cf. W. T. Stearn, Webbia 17: 207-222. 1962). Type: Peru, *Ruiz.*

Rhizome not seen; leaves subscandent or pendent with indeterminate growth, lamina elongate-lanceolate, bipinnate-pinnatifid, rachis atropurpureous, flexuous, pinnae elongate-deltoid, the basal ones deteriorated, the central ones longest and ascending, petiolulate, the stalks 12-25 cm. long, pinnules ovate or deltoid, the longer ones with few, blunt lobes, subcoriaceous, upper and lower surfaces with bright rust-colored sericeous tomentum, the trichomes with acuminate apex, ultimate segments bluntly lobed to crenulate, vein branches departing at moderately broad angles, the vein-ends flabellate, protruding in a tooth beyond the margin; spores dark brown.

The dense, reddish tomentum covering the leaf surfaces clearly distinguishes the species from others in the genus. Heavy tomentum of this type characterizes some species of the allied genus *Jamesonia* and illustrates a parallel development of the character in these two genera.

Peru and Colombia.

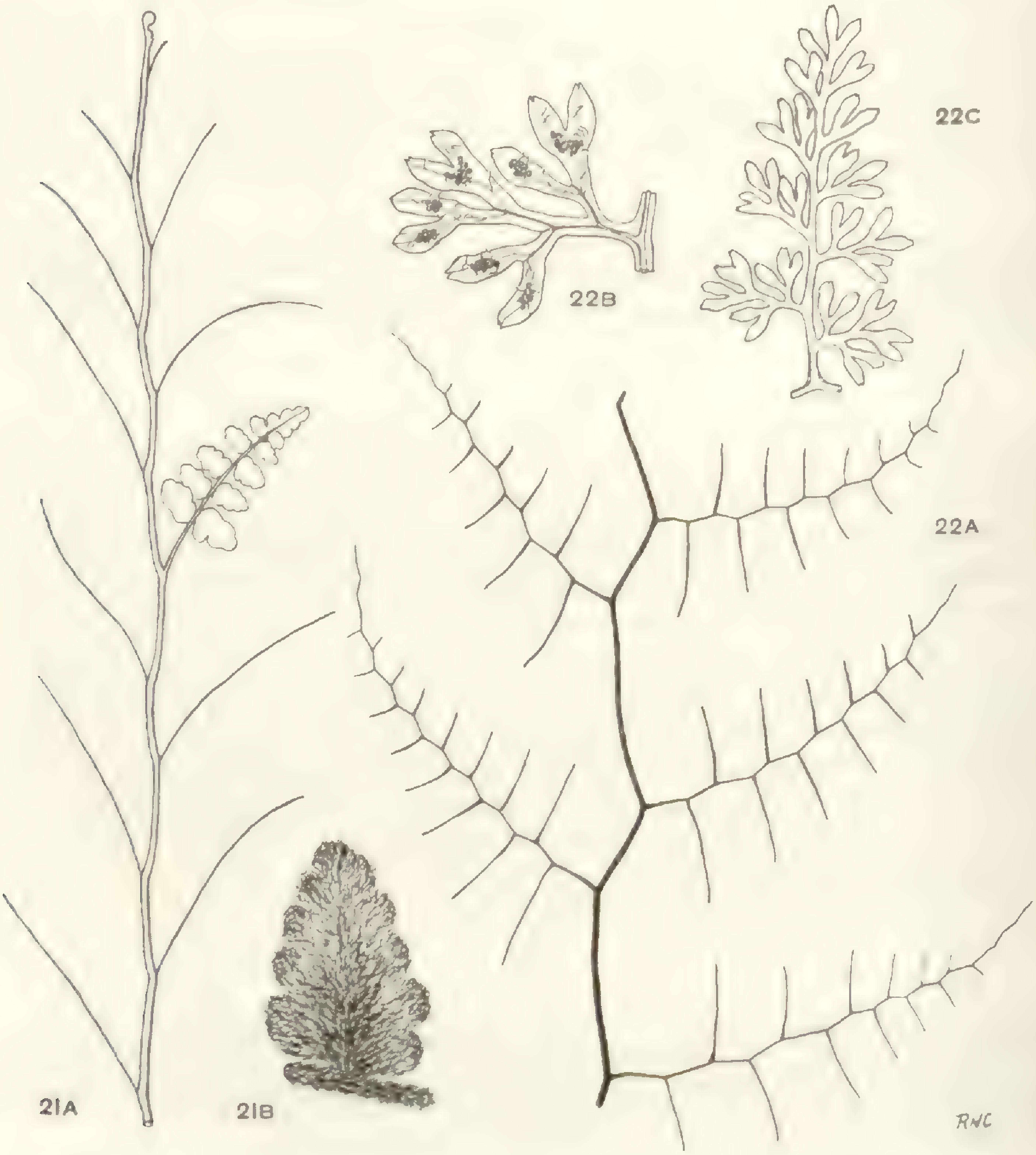
Open areas, on clay banks and in woods, Amazonas and Huánuco, 2750-3000 m.

Specimens seen: *Lobb* (K). AMAZONAS: Leimebamba to Balsas road, *Wurdack 1738* (GH). HUANUCO: Huánuco to Pampayacu, *Kanehira 152* (GH, US); Playapampa, *Macbride 4529* (F, US).

6. **Eriosorus flexuosus** (HBK.) Copel. Gen. Fil. 58. 1947. FIG. 22, MAP 4.

Gymnogramma flexuosa Desv. Ges. Naturf. Freunde Berlin Mag. 5: 306. 1811, ex char. Type: none cited. (Desvaux's epithet, although the earliest, cannot now be transferred to *Eriosorus*).

Grammitis flexuosa HBK. Nov. Gen. Sp. 1: 5. 1816, not HB. Pl. Aequin. 2: 167. 1809, as sometimes cited in error. Type: Venezuela, *Humboldt & Bonpland*, P! photo GH.



FIGS. 21-22. Fig. 21. *Eriosorus aureonitens:* A, architecture of lamina. × ¼. Peru, *Macbride 4529*, US; B, pinnule, × 1, *idem.* Fig. 22. *E. flexuosus:* A, architecture of central portion of lamina, × 1/3, Guatemala, *Steyermark 43078*, US; B, fertile segment, × 2½, *idem;* C, pinnule, × 1, *idem.*

Gymnogramma Ruiziana Kl. Linnaea 20: 410. 1847. Type: Prov. Panatahuarum, Peru, *Ruiz 74* B! photo GH.

Psilogramme flexuosa (HBK.) Kuhn, Fests. 50 Jub. Reals. Berol. (Chaetopt.) 339. 1882.

Gymnogramma flexuosa var. *peruviana* Hieron. Hedwigia 48: 220. 1909. Type: Cuesta de Lejia, prop. Molinobamba, Peru, *Stübel 1055*. B! photo GH.

Rhizome slender, elongate, 2-4 mm. in diam. with rigid, appressed, bristle or scale-like trichomes, with 1-10 cells at the base, dark brown to blackish, darker than the rhizome surface, with acuminate, rarely bulbous apical cell; leaves scandent, scrambling on other vegetation, indeterminate, sometimes exceeding 3 m. in length, lamina elongate, branching in several planes, 4-or 5-pinnate, rachis castaneous to straw colored, darker near the rhizome, flexuous, pinnae elongate, broadest near the rachis, petiolulate, pinnules ovate to deltoid, ascending or nearly at right-angles to the pinna-rachis, herbaceous, the upper and lower surfaces glabrous or sparsely pubescent, the trichomes clear or tan with acuminate apex, ultimate segments slender, usually several times longer than broad, bifid to deeply lobed, with 1 or 2 veins, vein branches departing at moderately broad angles, vein-ends not or slightly enlarged, extending to, or short of, the margin; spores usually dark brown, sometimes light brown.

There is considerable variation in the size of the ultimate segments in this species, although the ratio of length to breadth is relatively constant. The amount of indument on the lamina varies with age and with the location on the leaf. The size of segments also varies in different parts of the lamina. Such variation is difficult to interpret from herbarium specimens for most of them represent only pinnae or portions of the leaf apex.

Mexico, Central America; Hispaniola; British Guiana to Colombia, south to Bolivia.

Under trees and shrubs in moist areas, along river banks or mossy slopes, scrambling on other vegetation, Cajamarca to Cuzco, 2200-3600 m.

Selected specimens: CAJAMARCA: ne. of Socota, *Stork & Horton 10132* (F, UC). AMAZONAS: prope Molinobamba, *Stübel 1055* (B); 9 km. below Chachapoyas, *Wurdack 777* (GH); middle eastern Calla-Calla slopes, *Wurdack 1291* (GH). HUANUCO: Mito, *Bryan 205* (F), *Macbride & Featherstone 1829* (F, GH, US); Carpish, *Coronado 56* (US), *Ferreyra 10011* (GH), *Tryon & Tryon 5328* (GH, US); Huánuco to Pampayacu, *Kanehira 137* (GH), *139, 157* (US); Playapampa, *Macbride 4518* (F, US). HUANCAVELICA: Prov. Tayacaja, e. of Surcubamba, *Stork & Horton 10393* (F, GH). CUZCO: Río Urubamba valley, *Bües A30, A35*

MAPS 3-6. Map 3, *Hypolepis hostilis*. Map 4, *Eriosorus flexuosus*. Map 5, *E. elongatus*. Map 6, *Jamesonia*.

(US); Valle de Lares, *Bües 1906* (US); Convención, *Bües 2107, 2131* (US); Lucumayo valley, *Cook & Gilbert 1359* (US); Pillahuata, Cerro de Cusilluyoc, *Pennell 13941* (F, GH, NY); Paucartambo, *Vargas 1906* (GH, US). PUNO: entre Ayapata y Kahualluyoc, *Vargas 10750* (GH).

7. **Eriosorus Orbignyanus** (Kuhn) A. F. Tryon, Rhodora 65: 56. 1963. FIG. 23.

Gymnogramma Orbignyana Kuhn, Linnaea 36: 70. 1869. Syntypes: Yungas, Bolivia, *D'Orbigny 174*, B! photo GH (dupl. F!); Yorocares, Bolivia, *D'Orbigny 299*, B! photo GH.

Gymnogramma prehensibilis Baker, Syn. Fil. ed. 2, 517. 1874. Type: Sandillano, 8-9000 ft., Ecuador, *Pearce*, K! photo GH.

Rhizome not seen; leaves scandent, evidently indeterminate, lamina elongate, quadripinnate, rachis castaneous, lighter toward the apex, flexuous, pinnae elongate, broadest near the rachis, petiolulate, pinnules elongate-triangular, descending in an arc, herbaceous, the upper and lower surfaces sparsely pubescent, the trichomes clear with acuminate apex, more dense among the sporangia, ultimate segments as broad or broader than long broadly lobed to crenulate, with mostly 4-15 veins, vein branches departing at moderately broad angles, the vein-ends acute or clavate, extending to or nearly to the margin; spores dark to light brown.

This and the previous species are scandent with large, dissected leaves and in these characters they are superficially allied. They differ, however, in the form of the pinnules and ultimate segments, the position of the pinnules and other characters, and are probably not closely related.

Colombia to Bolivia.

Junín and Cuzco, 1500-2745 m.

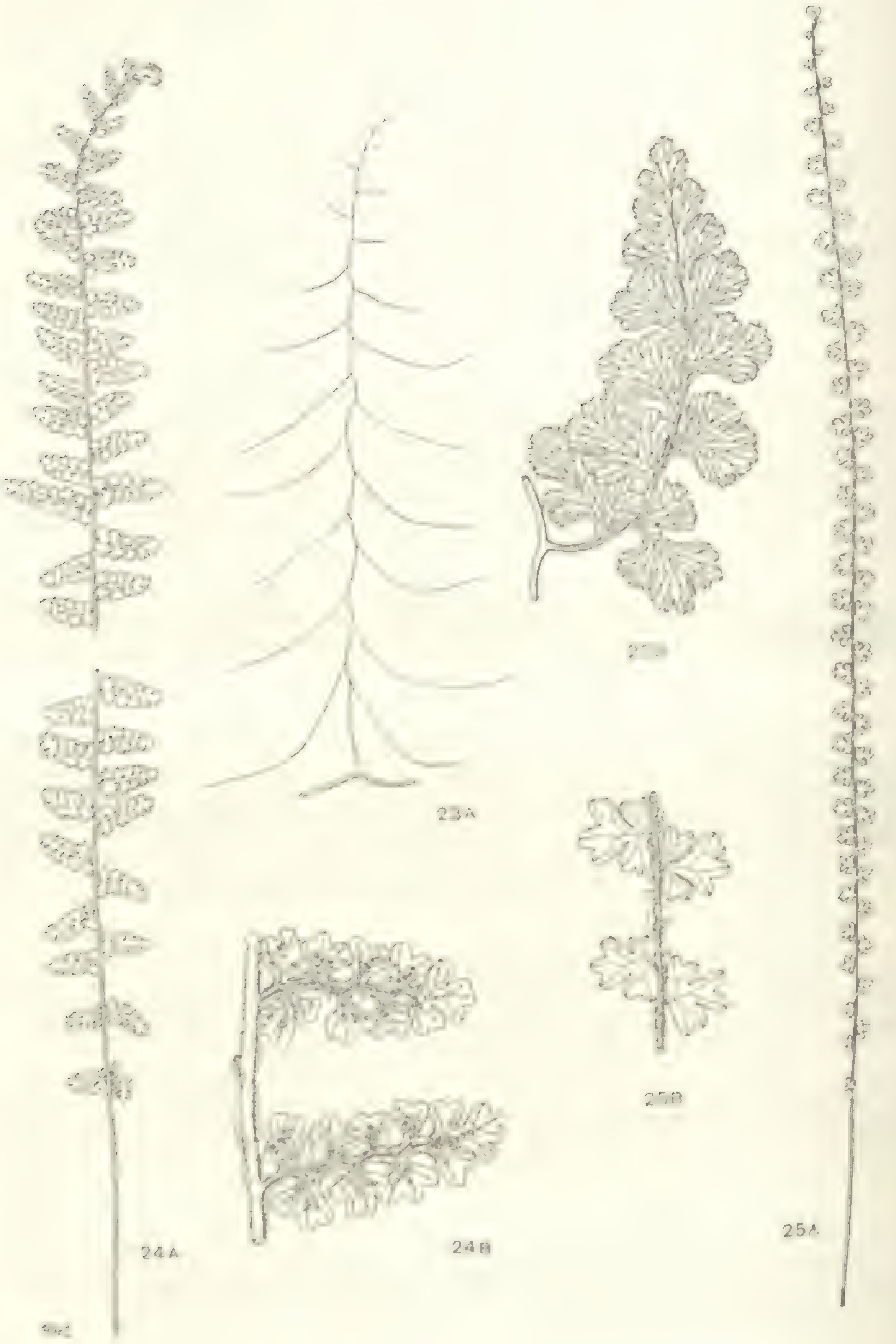
Specimens seen: JUNIN: Porvenir, *Killip & Smith 25947* (NY, US). CUZCO: Chaupimayo, *Bües 1949, 1950* (US).

8. **Eriosorus flabellatus** (Hook. & Grev.) Copel. Gen. Fil. 58. 1947. FIG. 24.

Gymnogramma flabellata Hook. & Grev. Jour. Bot. 1: 61, t. 120. 1834. Type: Surucucho, near Cuenca, 9000 ft., Ecuador, *W. Jameson*, E; isotype: K! photo GH, fragment US!

Psilogramme flabellata (Hook. & Grev.) Kuhn, Fests. 50 Jub. Reals. Berol. (Chaetopt.) 336. 1882.

Rhizome slender, elongate or compact, 2-4 mm. in diam., with rigid, appressed, bristle-like trichomes with 1-4, usually 1 or 2, cells at the base, darker than the rhizome surface, with an acuminate apex; leaves erect, indeterminate, lamina linear-elongate, 2-4 cm. wide, the base sometimes slightly narrowed, bipinnate-pinnatifid, rachis castaneous or



Figs. 23-25. Fig. 23. *Eriosorus Orbignyanus*: A, architecture of pinna, × ¼. Peru, *Buss 1009*, US; B, pinnule, × 1, *idem*. Fig. 24. *E. flabellatus*: lamina (central third omitted), × ½, Peru, *J. B. Steere*, US. B, pinnae, × 2, *idem*. Fig. 25. *E. elongatus*: A, lamina, × ½, Peru, *Tryon & Tryon 5319*, GH; B, pinnae, × 2, *idem*.

dark brown, lighter near the apex, straight, pinnae elongate-ovate or deltoid, petiolulate, usually with 4 or more pairs of pinnules 2-4 mm. distant, herbaceous with clear, multiseriate trichomes on both surfaces, longer and curled on the lower surface and usually appressed on the upper, the ultimate lobes bifid, vein branches departing at moderately broad angles, the vein-ends clavate or acute, ending short of the margin; spores light amber-colored or light brown.

This species is very close to *E. elongatus* and perhaps may better be regarded as a variety of it. The final treatment of these taxa awaits a more complete survey of variation throughout their ranges. In the northern portion of the range, *E. flabellatus* is more abundant than *E. elongatus*, while in Peru the latter is more abundant. The collections cited below are included in *E. flabellatus* mainly on the basis of the complexity of the pinnae and the spore color.

Colombia to Bolivia.

Specimens seen: Contumarca, *J. B. Steere* (GH, US); *Ruiz* (G, US).

9. **Eriosorus elongatus** (Hook. & Grev.) Copel. Gen. Fil. 58. 1947. FIG. 25, MAP 5.

Gymnogramma elongata Hook. & Grev. Jour. Bot. 1: 61, t. 119. 1834. Type: Surucucho, near Cuenca, 9000 ft., *W. Jameson*, E; isotype: K! photo GH.

Gymnogramma angustifrons Bak. Syn. Fil. 380. 1868, based on *Gymnogramma elongata* Hook. & Grev., not *Gymnogramma elongata* (Sw.) Hook. which is *Polypodium astrolepis;* an illegitimate new name for the earlier! homonym.

Psilogramme elongata (Hook. & Grev.) Kuhn, Fests. 50 Jub. Reals. Berol. (Chaetopt.) 335. 1882.

Rhizome slender or compact, 2-4 mm. in diam., with rigid, appressed bristle-like trichomes with 1-4, usually 1 or 2, cells at the base, darker than the rhizome surface, with a bulbous apex; leaves erect, indeterminate, lamina linear-elongate, 0.5-2.0 cm. wide, the base and apex sometimes narrowed, pinnate-pinnatifid, rarely bipinnate, rachis castaneous, lighter near the apex, straight, pinnae deltoid or ovate, rarely elongate-ovate, petiolulate, more or less lobed, rarely with stalked pinnules which are imbricate, herbaceous, with clear, multiseriate trichomes on both surfaces, rarely glandular, often longer and curled on the lower surface and appressed on the upper surface, the ultimate lobes bifid, vein branches departing at moderately broad angles, the vein-ends acute or clavate, extending to, or nearly to, the segment margin; spores dark brown.

The collections from Huánuco of Kanehira, Macbride, and Stork & Horton, are exceptional in having glandular indument on the lamina.

On rocky, foggy or dry slopes and road cuts or in open, grassy puna, Piura to Cuzco, 2500-3900 m.

Selected specimens: PIURA: above Huancabamba, *Hutchison 1616* (GH); e. of Huancabamba, *Weberbauer 6096* (F, GH, US). CAJAMARCA: pass s. of Conchán, *Stork & Horton 10072* (US). AMAZONAS: mts. e. of Balsas, *Osgood & Anderson 84* (F, US); Prov. Chachapoyas, summit of Puma-urcu, *Wurdack 1161* (GH). LIBERTAD: Prov. Bolivar, entre Unámen y Bolivar, *López & Sagástegui 3332* (GH); Las Quinuas, Longotea to Bolivar, *López & Sagástegui 3348* (GH). HUANUCO: Pampayacu, *Kanehira 143* (GH, US), *175* (US); Playapampa, *Macbride 4523* (F, US); Mito, *Macbride & Featherstone 1792* (F, US); Carpish, *Stork & Horton 9910* (F, GH), *Ferreyra 8172, 10033* (GH), *Hodge 6272* (GH); 35 km. ne. of Huánuco, *Tryon & Tryon 5319* (GH). AYACUCHO: Pampalca, *Killip & Smith 23249* (F, GH, NY, US); above Zanamonté, *Weberbauer 5658* (F, GH, US). CUZCO: Huadquiña, *Bües 978, 981* (US); Valle Lares, *Bües 1777* (US); La Convención, *Bües 2099, 2160* (US); Lucumayo Valley, *Cook & Gilbert 1360* (US); Cerro de Cusilluyoc, Paso de Tres Cruces, *Pennell 13850* (F, GH, NY, US); Paucartambo, *Vargas 12239* (GH).

FIG. 26. *Jamesonia peruviana*, Cordillera Vilcabamba (Cuzco).

7. **Jamesonia** Hook. & Grev. Icon. Fil. 2: t. 178. 1830. Type: *Jamesonia pulchra* Hook. & Grev. FIG. 26, MAP 6.

Terrestrial, the rhizome slender, creeping, pubescent or with bristle-like trichomes, bearing the leaves closely or widely spaced; leaves small to medium sized, pinnatisect to usually 1-pinnate, glabrous, glandular, pubescent or glandular-pubescent, veins free; sporangia borne along a portion (or most) of the veins, hardly or not covered by the reflexed, usually modified margin, indusium and paraphyses absent. — An American genus of 19 species.

Tryon, A. F., A monograph of the fern genus Jamesonia. Contrib. Gray Herb. 191: 109-197. 1962.

The treatment of this genus has been adapted by Alice F. Tryon from the monograph cited above. *Jamesonia* is a genus mainly of the páramos of Ecuador to Venezuela, where it is a characteristic element of the flora, and of the puna of Peru and Bolivia. The genus is characterized by the linear, elongate, often densely pubescent, leaves with indeterminate growth. In most species the margin is usually strongly enrolled with a modified membranaceous border which is entire or variously dentate or ciliate. This genus has clearly evolved from the previous one, *Eriosorus*, or from a common ancestor, and the two genera are not sharply differentiated. The unusual morphology and ecology of *Jamesonia*, however, justify their separation.

KEY TO SPECIES

a. Pinnae asymmetrical, inequilateral and usually cordate at the base; spores tan or light brown. .... b.
  b. Lower pinna surface with dense, matted tomentum. .... c.
    c. Apex of the lamina vermiform, with appressed trichomes, glandular and usually vernicose. .... 2. *J. Scammanae*
    c. Apex of the lamina about the same width or broader than the lower portions, with patent to slightly appressed trichomes, pubescent or tomentose. .... d.
      d. Pinnae, especially the older ones, convex on the upper surface (patelliform), glabrous or somewhat pubescent, the stalk at an oblique angle to the rachis. .... 1. *J. rotundifolia*
      d. Pinnae plane or with the basal lobes directed downward from the plane of the pinna, somewhat glandular on the upper surface, the stalk perpendicular to the rachis. .... 8a. *J. imbricata* var. *imbricata*

b. Lower pinna surface glabrous, glandular or with sparse trichomes. .... e.

e. Pinnae, especially the older ones, convex on the upper surface (patelliform), the stalk often bent, at an oblique angle to the rachis. .... 1. *J. rotundifolia*

e. Pinnae plane or slightly concave on the upper surface, the stalk straight, nearly perpendicular to the rachis. .... f.

f. Pinnae usually of a rigid-herbaceous texture, the upper surface conspicuously pubescent, with the epidermal cells unthickened; the lamina 0.3-0.7 cm. wide. .... g.

g. Upper pinna surface with long, appressed trichomes, especially on the distal portions, these usually enveloping several pinnae; the pinna margin with a wide, more or less papillate, border several cells broad. .... 3. *J. peruviana*

g. Upper pinna surface with short, erect, rigid, capitate trichomes; the pinna margin with a narrow border usually 1 cell broad, with cilia similar to the trichomes. .... 6. *J. boliviensis*

f. Pinnae coriaceous, the upper pinna surface glabrous, rarely with appressed glands or a few trichomes, with the epidermal cell walls thickened; the lamina usually about 1 cm. wide. .. h.

h. Lamina about the same breadth throughout or slightly narrower near the base; tomentum of the bud and rachis concolorous; the pinna margin with an contiguous border usually several cells broad. .... 4. *J. Alstonii*

h. Lamina clavate, broadest near the apex; tomentum of the apex and rachis bicolorous with a prominent dark streak; the pinna margin usually with an irregularly dentate border extended at the vein ends, not contiguous or scarcely so. .... 5. *J. Goudotii*

a. Pinnae symmetrical, the base equilateral; spores dark brown. ...... i.

i. Pinnae with slender stalks about 1 mm. long (or longer) and perpendicular to the rachis. .... j.

j. Pinna base cordate, lower surface of the pinna glandular or with a few short trichomes, the border narrow, usually of a single row of cells, ciliate, veins at wide angles, the branches often short. .... 7. *J. scalaris*

j. Pinna base truncate, lower surface of the pinna usually tomentose (to rarely glabrous), the border usually broad, dentate and/or ciliate, veins usually at acute angles, the branches long and somewhat parallel. .... 8b. *J. imbricata* var. *glutinosa*

i. Pinnae adnate, subsessile, or with short broad stalks less than 1 mm. long and at an oblique angle to the rachis, veins at acute angles, the branches long and nearly parallel. .... 9. *J. blepharum*

1. **Jamesonia rotundifolia** Fée, Mém. Fam. Foug. 7: 41, t. 10. 1857. Type: Colombia, *Schlim 363;* isotypes: G! K! P! photo GH. FIG. 27.

Rhizome trichomes castaneous or light brown, with 1 (-4) cells near the base; lamina ca. 14-65 cm. long, 0.7-1.5 cm. wide, about the same width throughout, the bud with trichomes patent or slightly appressed; pinnae rotundate-cordate, patelliform, especially the older pinnae, the margins enrolled, inequilateral at the base, herbaceous; upper surface more or less pubescent, especially the distal portion, the epidermal cell walls thickened, lower surface pubescent with tan or clear trichomes or glabrous, stalk bent at an oblique angle to the rachis, veins at acute to moderately wide angles, the branches long, border moderately broad, extended at the vein ends, irregularly dentate, sometimes little modified and similar to the pinna in texture; spores light tan.

This species represents one of the least specialized forms in the genus and can be readily distinguished by the large, straw-colored tomentum of the apical buds and the rotundate-cordate pinnae which have a patelliform shape, particularly in the older pinnae. It is known in Peru from two widely disjunct collections; the Huánuco station is the most southern extension of the species. It is expected that other records will be found since the species is one of the commoner ones in Colombia.

Costa Rica; Colombia to Peru.

Grassy steppe, Piura and Huánuco, 3200-3500 m.

Specimens seen: PIURA: e. of Huancabamba, *Weberbauer 6067* (B, F, GH, US). HUANUCO: Cushi, *Bryan 612* (F).

2. **Jamesonia Scammanae** A. F. Tryon, Contr. Gray Herb. 191: 164. 1962. Type: Cerro de la Muerte, Costa Rica, *Scamman & Holdridge 7929,* GH! FIG. 28.

Rhizome trichomes lustrous, light to dark brown, usually 1 (-5) cells near the base; lamina ca. 11-45 cm. long, 0.2-0.6 cm. wide, about the same size throughout, the bud vermiform, glutinous, with appressed trichomes; pinnae ovate, sometimes lobed, usually with a central furrow on the upper surface, the margin enrolled, inequilateral or nearly so at the base, upper surface glandular and vernicose or crustose, the epidermal cell walls unthickened, lower surface tomentose with whitish or tan trichomes, stalk bent, short to nearly absent, veins with broad to moderately broad angles, the branches moderately long, border moderately broad, entire or slightly undulate, firm-membranous or similar to the pinna texture; spores pale amber-colored or tan.

This species is readily recognized by the vermiform apex of the leaves and the nearly subsessile pinnae which are vernicose or crustose on the upper surface.

Costa Rica; Colombia to Bolivia.

In grassy uplands and among rocks, Lima and Huánuco to Puno, 2750-4270 m.

Specimens seen: HUANUCO: Huánuco, *Macbride & Featherstone 2182* (F, GH, US); Mito, *Bryan 183* (F, US). LIMA: Huarochiri, *Saunders 399* (BM). JUNIN: Acopalca, prov. Huáncayo, *G. Kunkel 485* (GH). APURIMAC: Abancay region, *Santander et al.* in 1935 (UC); Bosques de Ampay, *Vargas 1060* (GH). CUZCO: Sallcantay, *Bües 1008* (US); Piñasniocj, *Cook & Gilbert 1242, 1833* (US); Cerro de Cusilluyoc, *Pennell 13870* (F, GH, US); Paucartambo, *Soukup 386* (F); Achirani, Paucartambo, *Vargas 11165* (F, K, UC); entre Lares y Hierbabuinayoc, *Vargas 11999* (GH). PUNO: "Tabina," *Lechler 2032* (B, E, K, LE, P).

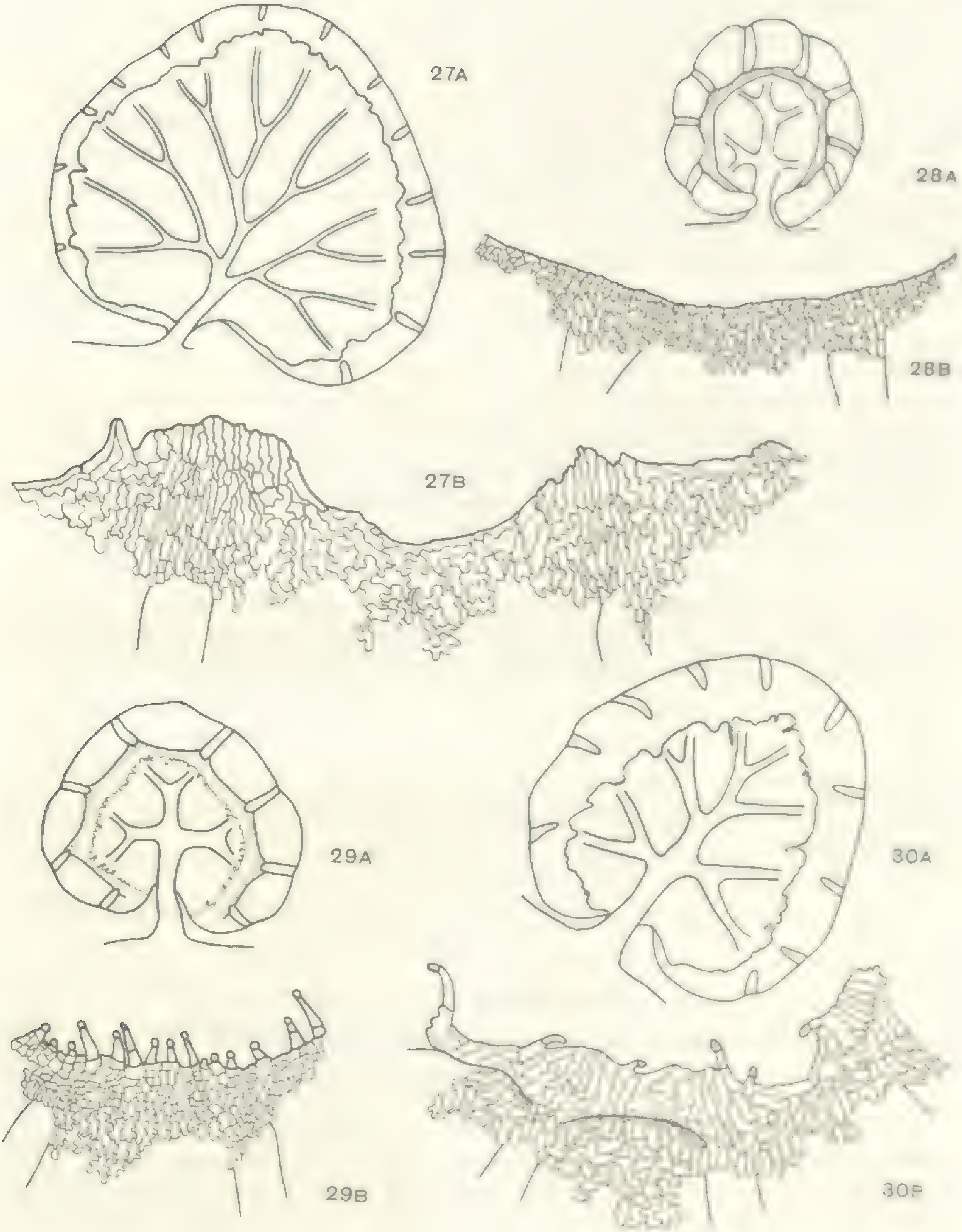
3. **Jamesonia peruviana** A. F. Tryon, Contr. Gray Herb. 191: 167. 1962. Type: Tambo de Vaca, Peru, *J. F. Macbride 4404*, F! FIGS. 26, 29.

Rhizome trichomes castaneous or atropurpureous, with 1 or 2 cells near the base; lamina ca. 17-40 cm. long, 0.3-0.5 cm. wide, broadest at the apex, the bud with tan or light brown patent or somewhat appressed trichomes, pinnae reniform or orbicular-cordate, concave on the upper surface, the margins enrolled, inequilateral at the base, rigid-herbaceous or slightly coriaceous, upper surface with long, discrete trichomes, strongly bent near the base of the trichome, appressed and usually enveloping several pinnae, with epidermal cell walls sometimes slightly thickened, lower surface with sparse, short, capitate, clear or tan trichomes and a tuft of longer trichomes on the stalk and adjacent veins, sometimes pubescent along all veins, stalk straight, perpendicular to the rachis, veins with wide angles, the branches short or moderately long, border broad, with more or less uniform papillae firm-membranous; spores tan or straw colored.

Jamesonia peruviana is a unique species having long, appressed trichomes on the upper surface of the pinnae and a rather uniform fringe of papillae on the border. The northernmost collection from Libertad differs from the others in having rather dense pubescense along the veins on the lower pinna surface and bulbous tipped rachis trichomes. Although the species is known from several collections, the early ones are incomplete and without locality data and most recent collections lack the rhizome. Ample and complete specimens of this species are much needed.

Peru and Bolivia.

In open grassy slopes, jalca, and in wet places, Amazonas to Puno, 3400-4300 m.



FIGS. 27-30. Fig. 27. *Jamesonia rotundifolia:* A, pinna, lower surface, × 5, Colombia, *Cuatrecasas 20223*, GH; B, pinna margin (two vein ends) × 35, Costa Rica, *Scamman & Holdridge 7928*, GH. Fig. 28. *J. Scammanae:* A, pinna, lower surface, × 10, Costa Rica, *Scamman & Holdridge 7929*, GH; B, pinna margin (two vein ends), × 35, Peru, *Vargas 1060*, GH. Fig. 29. *J. peruviana:* A, pinna, lower surface, × 10, Peru, *Pennell 13873*, GH; B, pinna margin (two vein ends), × 35, *idem*. Fig. 30. *J. Alstonii:* A, pinna, lower surface, × 10, Colombia, *Cuatrecasas 21884*, GH; B, pinna margin (three vein ends) (heavy lines indicate fold in the tissue), × 35, Ecuador, *Asplund 16856*, GH.

Specimens seen: *Dombey 18* (G, L, P), *Pavon 137* (G). AMAZONAS: Prov. Chachapoyas, summit of Cerros de Calla-Calla, *Wurdack 1216* (GH). LIBERTAD: Las Quinuas, *López & Sagástegui 3346* (GH). ANCASH: Huari, above Ponto, *Weberbauer 3302* (B, G, US). HUANUCO: Tambo de Vaca, *Bryan 648* (F, US). JUNIN: Tarma, *Née* (F); Muña, *Pearce*, in May 1863 (K). CUZCO: *Bües 1530, 1531* (US); Vilcabamba, *Bües 1598* (US); Convención, *Bües 2161*, in part (US); Cerro Cusilluyoc, *Pennell 13873* (F, GH, US); Tres Cruces, prov. Paucartambo, *Vargas 12240* (GH). PUNO: *Lechler 2153*, in part (B, E, G, K, LE, P, S-PA).

4. **Jamesonia Alstonii** A. F. Tryon, Contr. Gray Herb. 191: 168. 1962. Type: Los Farallones, del Valle, Colombia, *Cuatrecasas 21884*, GH! **Fig.** 30.

Rhizome trichomes usually dark brown or blackish, sometimes light brown, 1 (-4) cells near the base; lamina ca. 15-40 cm. long, 0.4-1.0 cm. wide, about the same width throughout or the base slightly narrowed, the bud with straw colored, matted or slightly appressed trichomes; pinnae ovate-cordate or orbicular-cordate, plane, the margins enrolled, inequilateral at the base, coriaceous, the upper surface glabrous, rarely glandular with epidermal cells thickened, lower surface with sparse short clear or tan trichomes and usually with a tuft of longer trichomes on the stalk and adjacent veins, stalk straight, perpendicular to the rachis, veins with wide angles, the branches short or moderately long, border moderately broad, extended at the vein ends, dentate, with sparse, short, bulbous cilia or entire, rigid-herbaceous; spores light amber-colored.

Jamesonia Alstonii most closely resembles *J. Goudotii* particularly in the coriaceous texture of the pinnae. There are several collections of it from Peru which are mixed with *J. peruviana* and these two must grow together. The collection of Stork and Horton from Libertad is exceptional in having dense glands on the upper pinna surface and very strongly enrolled margins.

Southernmost Mexico, Guatemala and Costa Rica; Colombia to Bolivia.

Under boulders in dry soil and among bunch grasses on wet slope, Libertad to Puno, 3355 and 4000 m.

Specimens seen: LIBERTAD: Huillias, north of Cachicadón, *Stork & Horton 10007* (F, G, K, UC). ANCASH: Condorcocha, prov. Bolognesi, *Cerrate 2547* (GH). HUANUCO: Mito, *Macbride & Featherstone 1883* (F, G, US). JUNIN: Huayllay, *Mathews 979* (E, GL, K). CUZCO: *Bües 1378* (US); Prov. Urubamba, camino a Sayacmarca, Aug. 1941, *C. Dreyfus* (GH). PUNO: *Lechler 2153*, in part (B, E, G, K, LE, P, S-PA).

5. **Jamesonia Goudotii** (Hieron.) C. Chr. Ind. Fil. 373. 1905. FIG. 31.

Gymnogramme Goudotii Hieron. Engl. Bot. Jahrb. 34: 476. 1904. Type: Colombia, *Goudot*, B! photo GH; isotype: G! photo GH.

Rhizome trichomes light brown to lustrous black, with usually 1 (-3) cells near the base; lamina ca. 5-40 cm. long, 0.5-1.2 cm. wide clavate, broadest at the apex, narrowed toward the base, the bud bicolorous, with erect or slightly appressed trichomes, these light brown and with a patch or streak of brown trichomes: pinnae reniform or orbicular-cordate, plane, or the margins incurved, sometimes strongly so, forming a pouch-like structure, inequilateral at the base, coriaceous, the upper surface usually glabrous, sometimes glandular, with epidermal cell walls thickened, lower surface with sparse, short, clear or tan, bulbous trichomes and a tuft of longer trichomes on the stalk and adjacent veins, stalk straight, perpendicular to the rachis, veins at wide angles, the branches moderately long, border irregularly dentate, usually extended at the vein-ends and ciliate, rarely entire or nearly so, rigid-herbaceous; spores tan or light amber-colored.

This species most closely resembles *J. Alstonii* and there are only slight differences between them in the form of the pinnae, the elaboration or the pinna margins and the color of the tomentum. At the Market in Huancayo a few leaves of *J. Goudotii* were obtained by Kunkel (*486*, GH).

In boggy places between rocks on a glacier, Junín and Cuzco, 3660-4500 m.

Specimens seen: JUNIN: Hacienda Runatullu, near Comas, *Weberbauer 6629* (F, GH, US). CUZCO: *Bües 1406* (US).

6. **Jamesonia boliviensis** A. F. Tryon, Contr. Gray Herb. 191: 174. 1962. Type: Bosques de Ampay, Apurímac, Peru, *Vargas 1060a*, GH! FIG. 32.

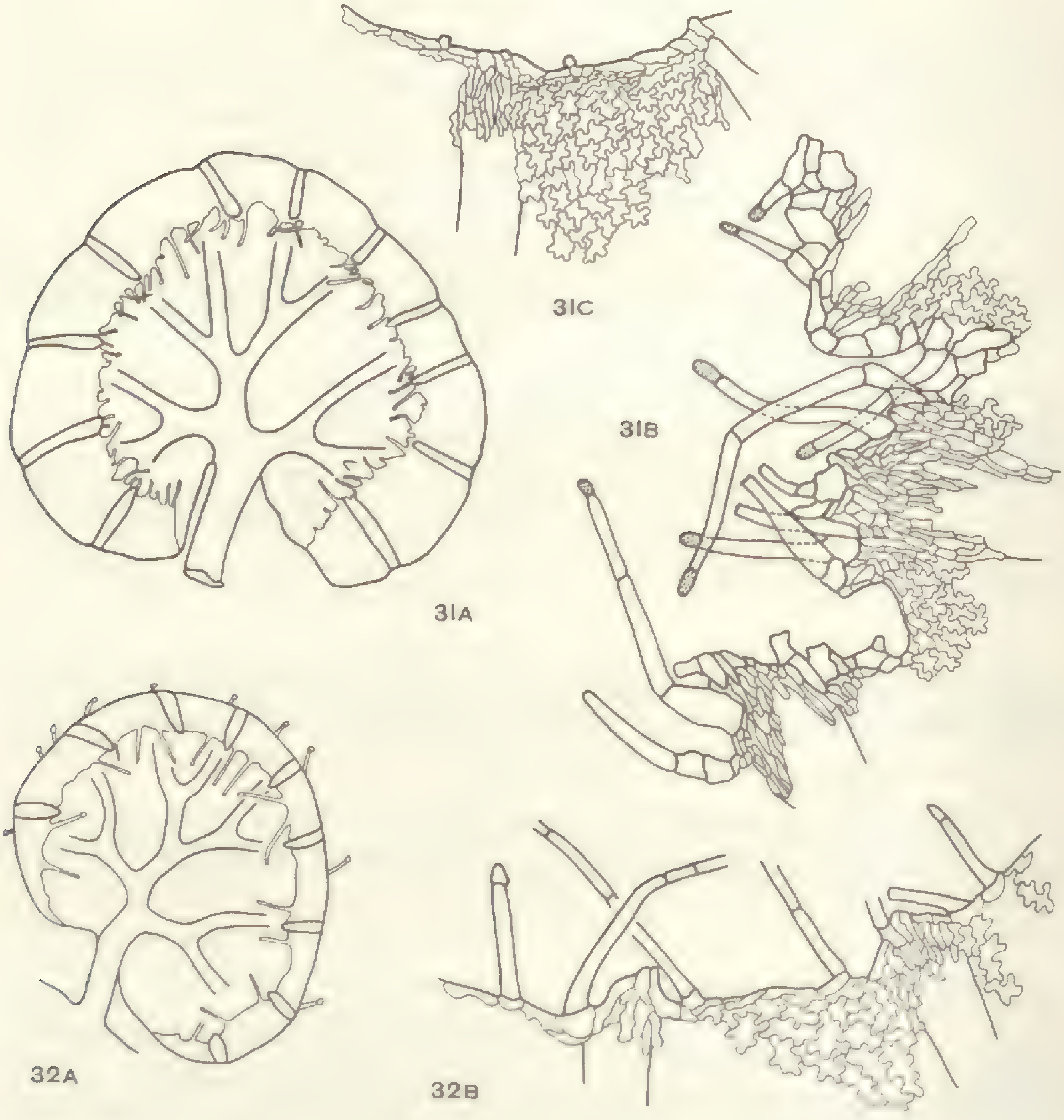
Rhizome trichomes lustrous atropurpureous or blackish, 2 or usually 1 cell at the base; lamina ca. 9-30 cm. long, 0.3-0.7 cm. wide, the same width throughout or the base slightly narrowed, the bud with rust-colored, patent trichomes; pinnae orbicular-cordate or ovate-cordate, plane, the margins incurved, inequilateral at the base, rigid-herbaceous, upper and lower pinna surfaces with short, clear, capitate trichomes with longer trichomes on the stalk and adjacent veins, the upper epidermis slightly thickened, stalk straight, perpendicular to the rachis, veins with wide angles, the branches short, or moderately long, border narrow, a row of cells mostly broader than long with capitate cilia; spores light amber-colored.

This species is unique in having the same form of indument on both surfaces of the pinnae and on the margin. The collections are mainly from Bolivia although the most complete and ample material, from César Vargas, has been designated as the type.

Peru and Bolivia.

"Woods," Apurimac, 3200 m.

Specimens examined: APURIMAC: Abancay region, Oct. 1935, *V. Santander et al.* (UC); Bosques de Ampay, *Vargas 1060a* (GH).



FIGS. 31-32. Fig. 31. *Jamesonia Goudotii:* A, pinna, lower surface, × 10, Colombia, *Cuatrecasas 19110*, GH; B, pinna margin (two vein ends), × 35, Colombia, *Mexia 7552*, GH; C, *idem*, Ecuador, *Penland & Summers 814*, US. Fig. 32. *J. boliviensis:* A, pinna, lower surface, × 10, Peru, *Vargas 1060a*, GH; B, pinna margin (two vein ends), × 35, *idem.*

7. **Jamesonia scalaris** Kze. Bot. Zeit. 2: 738. 1844. Type: Pillao, Peru, *Ruiz 49*, B! photo GH. FIG. 33.

Rhizome trichomes light to dark brown or atropurpureous, usually with 2 (-5) cells near the base; lamina ca. 10-33 cm. long, 0.2-0.5 cm. wide, about the same size throughout or the base slightly narrowed, the bud with tan or rust colored, patent or slightly appressed trichomes; pinnae ovate-cordate, usually lobed, patelliform, with the upper surface often depressed near the stalk, the margins enrolled, equilateral or nearly so at the base, herbaceous, the upper surface with papillate glands, the epidermal cell walls unthickened, lower surface with erect, clear or tan, capitate trichomes sometimes tomentose and usually with a tuft of trichomes on the stalk and adjacent veins, stalk straight or slightly bent perpendicular to the rachis, veins with wide angles, the branches short or moderately long, border narrow, a row of cells mostly broader than long and with capitate cilia; spores dark brown.

This species is readily distinguished from the others in Peru with small pinnae, by the patelliform and lobed form of the pinnae, the glands on the upper surface and the dark spores. It appears to grow with *J. peruviana* and *J. Scammanae* for these species are sometimes mixed in collections.

Peru and Bolivia.

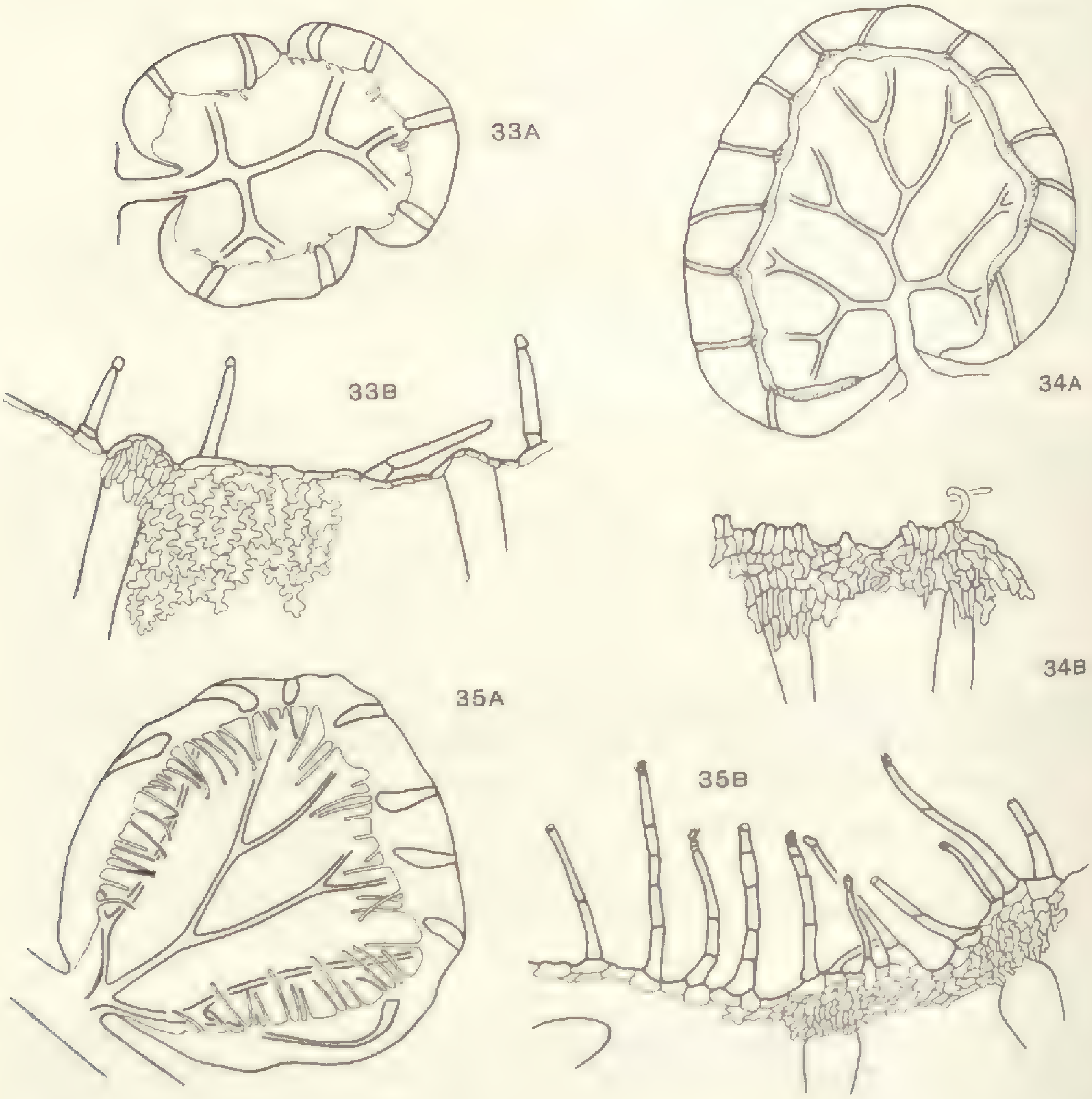
In sphagnum, montaña on moist slopes, Libertad to Puno, 2750-4270 m.

Specimens seen: Pacechac, *Hill 553* (K). LIBERTAD: Pumatambo, Puerta del Monte, prov. Pataz, *López & Sagástegui 3435* (GH). HUANUCO: Punta de Panao, *Asplund 13718* (GH, S); Playapampa, *Macbride 4524* (F, US). PASCO: Goyllarisquisca, *Asplund 11922* (GH, S). JUNIN: Tarma, *Pavon 137* (G). CUZCO: *Bües 1533, 1783, 1784, 1931, 2163* (US); La Convención *Bües 2161*, in part (US); Cochapatu, *Bües 2190* (US); Marcapata, *Stafford 989* (K); Paucartambo, June, 1937, *Vargas* (GH). PUNO: Ayapata, *Lechler 2036a* (B, E, G, K, LE, P).

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

Rhizome trichomes tan or ruddy brown to blackish, with 1 (-3) cells near the base; lamina ca. 7-80 cm. long, 0.2-1.2 cm. wide, about the same width throughout, the bud with tan, brown or bicolorous, patent or appressed trichomes; pinnae orbicular, ovate, patelliform, or the upper surface plane or sunken, the margins enrolled, equilateral and truncate and incurved at the base or slightly inequilateral and somewhat cordate, rigid-herbaceous, upper surface glandular sometimes also with a few trichomes, rarely glabrous, the cell walls unthickened, lower surface tomentose with clear, white or rust colored trichomes, stalk usually bent or twisted sometimes nearly straight, perpendicular to the rachis; veins with acute angles and the branches long, or with wide angles and moderately long; border moderately broad, entire or dentate and sparsely ciliate; spores tan or light to dark brown.

The species is known with certainty in Peru only from recent collections of var. *glutinosa* in Amazonas. Variety *imbricata* is recorded from Peru by the type collection of J. Jussieu but the locality for this material is not certain. A third variety, var. *meridensis*, occurs in the Andes of Venezuela.



FIGS. 33-35. Fig. 33. *Jamesonia scalaris:* A, pinna, lower surface, × 10, Peru, *Asplund 13718*, GH; B, pinna margin (two vein ends), × 35, Peru, *Bües 2163*, US. Fig. 34. *J. imbricata* var. *imbricata:* A, pinna, lower surface, × 10, Peru, *Jussieu*, P; B, pinna margin (two vein ends), × 35, *idem*. Fig. 35. *J. blepharum:* A, pinna, lower surface, × 10, Peru, *Kanehira 148*, GH; B, pinna margin (three vein ends), × 35, *idem*.

8a. Jamesonia imbricata var. imbricata FIG. 34.

Pteris orbiculata Poir. Lam. Encycl. 5: 710. 1804, not Houtt. Nat. Hist. 14: 108. 1783. Type: "Pérou", *J. Jussieu* (Herb. Jussieu no. 1332) P! photo GH.

Pteris imbricata Sw. Syn. Fil. 102. 1806, based on *Pteris orbiculata* Poir.

Rhizome trichomes amber colored or light tan, lighter than the rhizome surface; lamina indeterminate, the bud of the same size or larger than the mature pinnae with tan or light brown, patent trichomes; pinnae orbicular or ovate, the upper surface plane or sunken, slightly inequilateral at the base and somewhat cordate, the upper surface somewhat glandular sometimes also with a few trichomes, lower surface tomentose with rust or tan colored trichomes, stalk slightly bent, veins with wide angles, the branches widely diverging, moderately long, border rust colored or tan; spores tan or light brown, sometimes shriveled.

This variety is known from Peru only by the type collection. There is a rather unusual combination of characters in this material and a few other collections from Colombia and Ecuador are identified as this variety.

Peru, Ecuador and Colombia, 3385-3400 m.

Specimen seen: Herb. Jussieu 1332 (P).

8b. Jamesonia imbricata var. glutinosa (Karst.) A. F. Tryon, Contrib. Gray Herb. 191: 182. 1962.

Jamesonia glutinosa Karst. Fl. Columb. 2: 85, t. 143. 1865. Type: monte Guadalupé, Bogotá, Colombia, *H. Karsten*, LE! photo GH.

Rhizome trichomes ruddy to dark brown, the same color or more ruddy than the rhizome surface; lamina usually indeterminate, the bud usually smaller than the mature pinnae with tan, brown or usually bicolorous, appressed or patent trichomes; pinnae orbicular or ovate, patelliform, with the base equilateral, truncate and incurved adjacent to the stalk, upper surface usually glandular and vernicose, rarely glabrous, lower surface with clear, opaque, white or tan trichomes, sometimes nearly glabrous, stalk strongly bent, veins with acute angles, the branches long and somewhat parallel, border whitish or tan; spores dark brown.

This variety is relatively widespread in the Andes from Venezuela to Colombia but has just recently been discovered in northern Peru. It has undoubtedly been overlooked earlier for it is noted to be locally abundant. Plants in Venezuela and Colombia are quite variable, particularly where they occur with other species. Characters such as rhizome indument, the size, shape, border and indument of the pinnae, which are fairly constant in other species, are variable in these plants. The bent pinnae stalks, the patelliform shape of the pinnae and their equilateral base with truncate margins at the stalk and the dark brown spores best characterize this variety.

Venezuela to Colombia, south to Peru.

In open scrub forest and at the base of rocks, Amazonas, 3100-3300 m.

Specimens seen: AMAZONAS: Prov. Chachapoyas, Cordillera Callacalla, Leimebamba to Balsas, *López, et al. 4447, 4448* (GH); Summit of Puma-urcu, se. of Chachapoyas, *Wurdack 1160* (GH).

9. **Jamesonia blepharum** A. F. Tryon, Contrib. Gray Herb. 191: 190. 1962. Type: Pampayacu, Huánaco, Peru, *Ryozo Kanehira 148*, GH! FIG. 35.

Rhizome trichomes lustrous, light to dark brown or atropurpureous, with 1 or 2 cells near the base; lamina ca. 10-55 cm. long, 0.5-1.0 cm. wide, the lamina nearly the same width throughout or the base and apex more slender, sometimes determinate, the bud with dark brown, appressed, glutinous trichomes; pinnae orbicular, entire, usually patelliform, the margins incurved or enrolled, equilateral at the base, rigid-herbaceous, the upper surface vernicose with appressed glands, with epidermal cell walls sometimes thickened, lower surface with erect, capitate, clear or tan trichomes, these usually longer on the veins, sometimes curled and matted, stalk oblique (if present), often broad and decurrent on the upper surface of the rachis, veins with acute angles, the branches long, nearly parallel, border narrow, a row of cells broader than long, ciliate; spores dark brown.

This species is readily distinguished from others in Peru by the nearly adnate pinnae with long nearly parallel veins and ciliate margins.

Colombia to Bolivia.

Huánuco and Cuzco, 2900 m. and 4575 m. respectively.

Specimens seen: HUANUCO: Carpish, entre Huánuco y Tingo María, *Ferreyra 6702* (GH). CUZCO: *Bües 1824, 1914* (US); Valle de Lares, *Bües 1908* (US).

8. PTEROZONIUM Fée, Mém. Soc. Mus. Hist. Nat. Strasbourg 4: 202. 1850. Type: *Gymnogramma reniformis* Mart. = *Pterozonium reniforme* (Mart.) Fée.

Terrestrial, the rhizome small to moderately stout, short-creeping, densely pubescent, bearing the leaves in a rosette or loose cluster; leaves small, the lamina entire, reniform to orbicular-cuneate, glabrate, veins free; sporangia borne for a short distance along the veins, forming a band well back of the hardly modified margin, intermixed with short trichomes, indusium absent. — A South American genus of 5-7 species.

Pterozonium reniforme (Mart.) Fée, Gen. Fil. 178, 385. 1852. FIG. 37.

Gymnogramma reniformis Mart. Icon. Crypt. Bras. 88, t. 26. 1834. Type: Mt. Cupatí, Río Japurá, Brazil, *Martius.*

Rhizome trichomes yellowish brown to reddish brown, many cells long, one cell wide, gland-tipped; leaf ca. 5-20 cm. long, the long petiole dark reddish brown to blackish, with a pale ridge on each side extending down from the base of the lamina; lamina coriaceous, the outer margin crenulate, with a cartilaginous border.

Brazil and Peru.

Very rare on acidic rocks in San Martín and western Loreto, 1000 m.

Specimens seen: SAN MARTIN: Monte Guayrapurima, Tarapoto, *Spruce 4641* (B, GH, K, NY). LORETO: Cerro de Isco (evidently between Yurimaguas and Tarapoto), *Ule 6887* (B, P); Cuesta de Yento, near Balsa Puerto, *Raimondi 25* (B).

9. PITYROGRAMMA Link, Handb. Gewächse, 3: 19. 1833. Type: *Acrostichum chrysophyllum* Sw. = *Pityrogramma chrysophylla* (Sw.) Link. FIG. 36.

Ceropteris Link, Fil. Sp. Cult. 141. 1841. *(nom. superfl., illegit.)*

Trismeria Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 164. 1852. Type: *Trismeria aurea* Fée = *Acrostichum trifoliatum* L. = *Pityrogramma trifoliata* (L.) Tryon.

Terrestrial, the rhizome small to often stout, erect or decumbent, scaly, especially at the apex, bearing the leaves in a crown or cluster; leaves of medium size to large, 1-pinnate to tripinnate, usually with white or yellow ceraceous indument beneath, less often pubescent, rarely glabrous, veins free; sporangia borne along the veins, somewhat back of the nearly unmodified margin, at maturity often confluent over most of the surface, indusium and paraphyses absent. — 12 American species.

Domin, K. The hybrids and garden forms of the genus Pityrogramma (Link), Rozpr. II. Tr. Ceské. Akad. 38(4). 1929.

Tryon, R. Pityrogramma (including Trismeria) and Anogramma, Tax. Fern Notes II, Contrib. Gray Herb. 189: 52-76. 1962.

Some of the species grow in open habitats and on road banks and in other disturbed places. Many are adaptable to horticulture and were widely cultivated in the 19th century as ornamentals. The species with white or bright yellow indument were especially popular and were known as silver ferns and gold ferns. A somewhat confused account of the numerous horticultural forms is found in Domin's publication.

FIG. 36. *Pityrogramma calomelanos*, Iquitos (Loreto).

KEY TO SPECIES

a. Secondary and tertiary segments (if present) moderately, if at all, toothed, or with broad lobes with several veins. .... b.

b. Vascular bundles of the petiole (at about 1/3rd the distance to the lamina) roundish, oval to C-shaped; pinnae with numerous, pinnately arranged lobes or segments. .... c.

c. Petiole, primary rachis and secondary rachises glabrous, ceraceous or thinly and irregularly pubescent. .... d.

d. Rachis and petiole deep reddish brown to blackish; scales of the apex of the rhizome and the base of the petiole with a long portion one cell wide below the terminal cell. .... e.

e. Pinnae equilateral, the pinnules ascending, those on the basiscopic side more strongly so than those on the acroscopic side; scales of the apex of the rhizome and the base of the petiole with a long-conical terminal cell. .... 1. *P. calomelanos*

e. Pinnae inequilateral, the pinnules, on both sides of the pinna, at nearly right-angles to the pinna-rachis (or in large leaves the tertiary segments so disposed on the pinnule-rachis); scales of the apex of the rhizome and the base of the petiole with a spherical terminal cell. .... 2. *P. tartarea*

d. Rachis and the upper portion of the petiole, or all of it except the base, straw colored to light brown; scales of the apex of the rhizome and the base of the petiole with only a short portion one cell wide below the spherical terminal cell. .... 3. *P. chrysoconia*

c. Primary rachis and secondary rachises densely and persistently lanate, the petiole similar but sometimes deciduously lanate. .... 4. *P. ferruginea*

b. Vascular bundles of the petiole (at about 1/3rd the distance to the lamina) C-shaped with the back of the C curved forward. .... 5. *P. trifoliata* and hybrids of it.

a. Secondary and tertiary segments strongly laciniate into linear lobes, each with one vein. .... 6. *P. Pearcei*

1. **Pityrogramma calomelanos** (L.) Link, Handb. Gewächse 3: 20. 1833.

Rhizome scales (and those at the base of the petiole) with a long portion, one cell wide, below the long-conical terminal cell; leaf ca. 0.5-1 m. long, its axes glabrous to thinly ceraceous or thinly pubescent, petiole and the rachis deep reddish brown to blackish; lamina usually narrowly lanceolate to ovate-lanceolate, to long-triangular, pinnate-pinnatisect to tripinnate, pinnae equilateral, equally developed on both sides, pinnules ascending, the lower surface rarely glabrous, usually white, lemon-yellow, bright-yellow, orange-yellow or pale roseate ceraceous, or pubescent.

Two of the varieties, *aureoflava* and *ochracea* usually grow in the Andes above 1500 m., while var. *calomelanos* typically grows below 1000 m. It is widely distributed through the American tropics and seems to grow more rapidly and is more often an occupant of disturbed habitats than the other varieties.

Some specimens of *P. calomelanos* and *P. tartarea* are not easily distinguished and some characters additional to those presented in the key to species are mentioned under the latter species.

1a. Pityrogramma calomelanos var. calomelanos. FIGS. 36, 38, MAP 7.

Acrostichum calomelanos L. Sp. Pl. 2: 1072. 1753. LINN sheet 1245.19, photo A, GH, is this species.

Gymnogramma calomelanos var. *denudata* Harr. Jour. Linn. Soc. Bot. 16: 37. 1877. Type: Pébas, Peru, *Steere*, K! photo GH.

Lamina ceraceous beneath, the wax white to pale (lemon) yellow or pale roseate; or rarely the lamina glabrous.

Southern Florida; Greater and Lesser Antilles; Mexico to Panama; French Guiana west to Colombia, Ecuador and Galápagos Islands south to Bolivia and Argentina; Paraguay and Brazil.

Cleared hillsides, road banks, river banks, thickets and sometimes in forests, Tumbes to Cuzco, 100-1500 m., most commonly below 1000 m.

Selected specimens: TUMBES: between Tumbes and Caucho, *Coronado 224* (GH, UC). AMAZONAS: Aramango, prov. Bagua, *López et al. 4161* (GH). SAN MARTIN: 4 miles e. of Tarapoto, *Woytkowski 35212* (UC); Lamas, near Tarapoto, *L. Williams 6360* (F, GH). LORETO: Caballo-cocha, *L. Williams 2201* (F, GH); Santa Ana, upper Río Nanay, *L. Williams 1257* (F); above Pongo de Manseriche, *Mexia 6101* (F, GH, UC); Iquitos, *Tryon & Tryon 5167* (BM, F, GH, U, US, USM); Boquerón Padre Abad, *Woytkowski 34379* (UC); Yurimaguas, *Killip & Smith 27961* (US); Gamitanicocha, Río Mazán, *Schunke 224* (F, GH, UC, US); Hacienda San Jorge, 55 km. w. of Pucallpa, *Ferreyra 13008* (GH, USM); Paraiso, alto Río Itaya, *L. Williams 3212* (F); Pumayacu, between Balsapuerto and Moyobamba, *Klug 3247* (F, GH, US); Pébas, Río Amazonas, *L. Williams 1780* (F), *Steere* (GH). HUANUCO: Tingo María, *Soukup 2188* (F), *Ferreyra 10059A* (GH, USM), *Tryon & Tryon 5244* (BM, F, GH, U, US, USM); Hacienda Exito, *Mexia 8167* (F, GH, UC, US); Pampayacu, *Kanehira 145* (GH, US); Pozuzo, *Macbride 4616* (F, US); Villcabamba, *Macbride 4988* (F, US). JUNIN: San Ramón, *Coro-*

nado 267 (UC); Puerto Yessup, *Killip & Smith 26254* (F, US); La Merced, *Killip & Smith 23389* (US). AYACUCHO: Río Apurímac valley, near Kimpitiriki, *Killip & Smith 22958* (US). CUZCO: Hacienda Cadena, valle de Marcapata, *Scolnik 945* (US); Valle de Marcapata, *Herrera 1199* (US); Machu-Picchu to Quillabamba, *Mexia 8089a* (UC).

1b. **Pityrogramma calomelanos** var. **aureoflava** (Hook.) Bailey, Man. Cult. Pl. 64. 1926. MAP 8.

Gymnogramma calomelanos var. *aureoflava* Hook. Gard. Ferns, t. 50 text. 1862. Lectotype: *Seeman 948*, K.

Pityrogramma austroamericana Domin, Publ. Fac. Sci. Univ. Charles 88: 7. 1928. (Also Kew Bull. 1929: 221.) Lectotype: Bolivia, *Mandon 1549 bis*, K! photo GH; isotype: GH!

Pityrogramma calomelanos var. *austroamericana* (Domin) Farw. Am. Midl. Nat. 12: 280. 1931.

Lamina ceraceous beneath, the wax bright yellow to orange-yellow.

Costa Rica; Venezuela, Colombia, Ecuador and Galapagos Islands south to Bolivia and northwestern Argentina; Brazil.

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MAPS 7-8. Map 7, *Pityrogramma calomelanos* var. *calomelanos*. Map 8, *P. calomelanos* var. *aureoflava*.

Open, rocky places, grassy slopes, clay banks, thickets and rarely along irrigation ditches (Libertad), Lambayeque and Cajamarca to Cuzco, 680-2200 m.

Specimens seen: LAMBAYEQUE: 32 km. from Olmos, on road to Jaén, *Correll & Smith P831* (GH); 25 km. from Olmos, on road to Jaén, *Correll & Smith P799* (GH). CAJAMARCA: entre Abra de Porculla y Jaén, *Ferreyra 13638* (GH, USM). LIBERTAD: Hacienda Mochal, prov. Trujillo, *Sagástegui 425* (GH); Campiña de Moche, *López 1311* (GH); Huaranchal, *Sagástegui 94* (GH). HUANUCO: between Chinchao and Puente Durand, *Coronado 89* (GH, UC); Yanano, *Macbride 3667* (F, US). JUNIN: La Merced, *Soukup 2368* (F, GH), *3410* (GH, US), *Killip & Smith 23801* (F, US); Colonia Perené, *Killip & Smith 24984* (US). AYACUCHO: Aina, between Huanta and Río Apurímac, *Killip & Smith 22697* (F, GH, US). CUZCO: Pumachaca, valle de Santa Ana, *Herrera 3288* (GH, US); Torontoy, *Herrera 1333* (US); Valle de Lacco, *Herrera 2072* (US); Santa Rosa, Urubamba valley, *Cook & Gilbert 1728* (US); Machu-Picchu, *Vargas 2154* (US), *Coronado 106* (UC); valley of the Sambray, *Mexia 803* (US); near Quillabamba, *Mexia 8045* (F, GH, US); Potrero, 8 km. w. of Quillabamba, *Tryon & Tryon 5365* (BM, F, GH, U, US, USM), *Vargas 1739* (GH).

1c. **Pityrogramma calomelanos** var. **ochracea** (Presl) Tryon. Contrib. Gray Herb. 189: 61. 1962. FIG. 39, MAP 9.

Gymnogramma ochracea Presl, Rel. Haenk. 1: 17. 1825. Type: Peru, *Haenke*, PR (Herb. no. 24360), photo GH, US; probable isotypes: K fragment NY!, B fragment NY!

Gymnogramma Ballivianii Rosenst. Fedde Repert. 6: 314. 1909. Type: Bolivia, *Buchtien 1038*, S-PA! fragment ex Rosenst. US!

Ceropteris adiantoides var. *peruviana* Hieron. Hedwigia 48: 221. 1909. Type: Peru, *Stübel 1096*, B, not *P. calomelanos* var. *peruviana* (Desv.) Farw.

Pityrogramma ochracea (Presl) Domin, Publ. Fac. Sci. Univ. Charles 88: 8. 1928.

Pityrogramma Ballivianii (Rosenst.) Domin, *op. cit.*: 10.

Pityrogramma perelegans Domin, *op. cit.*: 8. Type: Tarapoto, Peru, *Spruce* in 1855-56, K! photo GH.

Lamina pubescent beneath, not ceraceous.

The spores of some specimens of var. *ochracea* have well defined dark ridges typical of the genus. Other specimens have spores that are more spherical than the usual type, although somewhat flattened in three planes on the commissural face, and the tan exospore is smooth or only slightly roughened. It is exceptional to find such different spores in the same species or variety.

A hybrid of var. *ochracea* and *P. trifoliata* is treated under that species.

Honduras; Venezuela to Colombia, south to Bolivia.

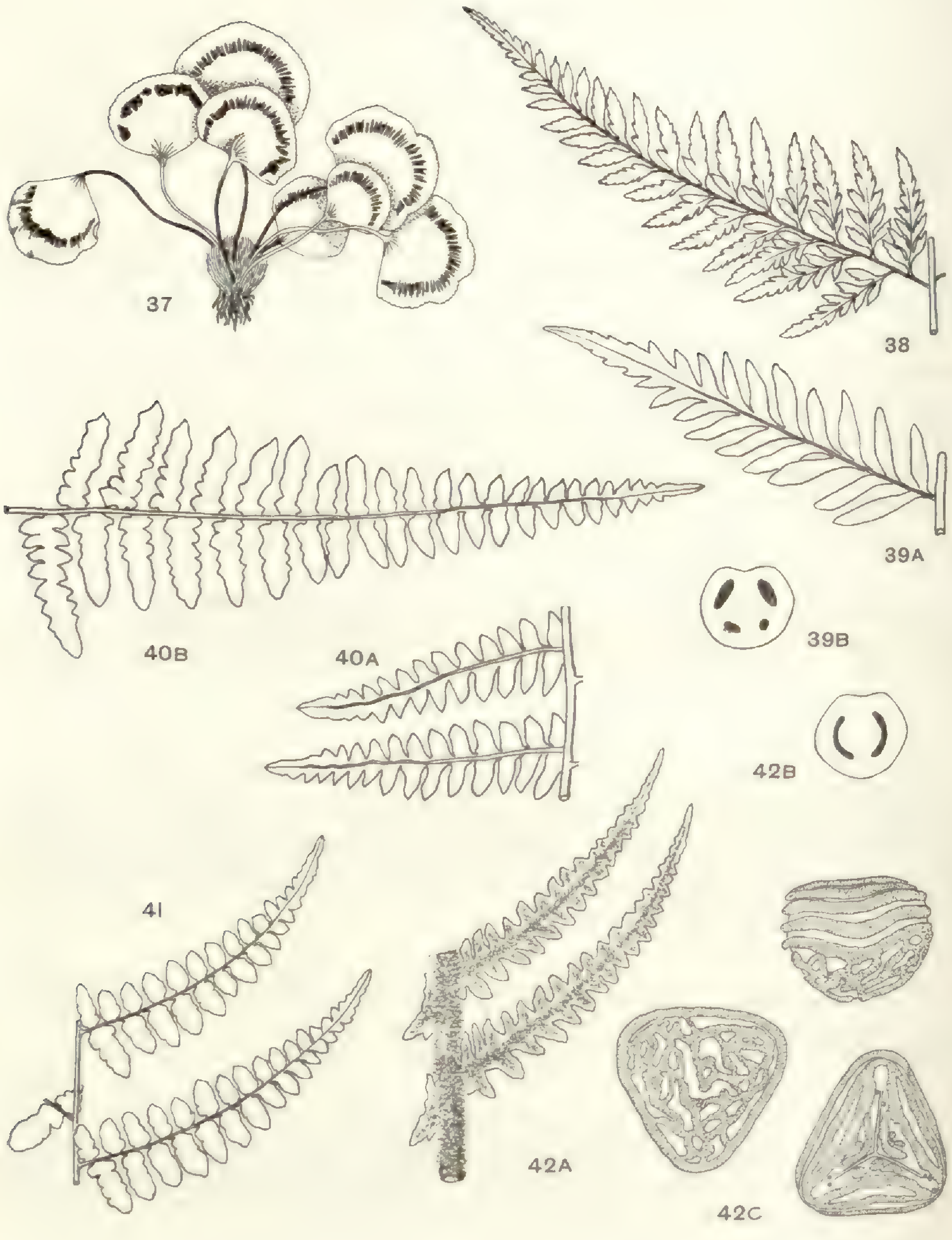
Open rocky places, river banks and road banks, cleared hillsides, cliffs, less often in thickets, forest or along forest borders, rarely along irrigation ditches, San Martín to Puno, 400-2600 m. or at 50 m. along irrigation ditches in Libertad.

Selected specimens: SAN MARTIN: near Moyobamba, *Woytkowski 35314* (UC); Juan Jui, alto Río Huallaga, *Klug 4177* (F, GH, UC); Divisoria, Aug. 3, 1942, *Ridoutt* (GH, USM). LORETO: Boquerón Padre Abad, *Allard 22106, 22070* (GH, US). LIBERTAD: Huaca del Sol, *Sagástegui 393* (GH); Hacienda de Mochal, *Sagástegui 425a* (GH); between Poroto and Samne, *Angulo & López 464* (GH); Mampuesto, *López 1313* (GH). HUANUCO: entre Puente Durand y Chinchavito, *Ferreyra 6787* (GH, USM); Puente Durand, *Stork & Horton 9446* (F, UC); Villcabamba, *Macbride 4994* (F, GH, US); Tingo María, *Tryon & Tryon 5243* (BM, F, GH, U, US, USM); Hacienda Exito, *Mexia 8166* (F, GH, US). PASCO: Oxapampa, *Soukup 2360* (GH). JUNIN: La Merced, *Macbride 5276* (F, US), *Soukup 3411* (GH), *Cerrate 2833* (GH, USM); Colonia Perené. *Killip & Smith 25421* (F, US); San Ramón, *Coronado 267* (GH); Carpapata, *G. Kunkel 591* (GH). AYACUCHO: Estrella, between Huanta and Río Apurímac, *Killip & Smith 22667* (US). CUZCO: Machu-Picchu, *Herrera 3301* (GH, US); Pumachaca, valle de Santa Ana, *Herrera 3288a* (US); Potrero, 8 km. w. of Quillabamba, *Tryon & Tryon 5366* (BM, F, GH, U, US, USM); Machu-Picchu to Quillabamba, *Mexia 8089* (F, GH, US); Santa Rosa, *Cook & Gilbert 1715* (US); Cosñipata, *Vargas 11293* (GH). PUNO: near Puno, *Soukup 449* (F).

2. **Pityrogramma tartarea** (Cav.) Maxon, Contrib. U. S. Nat. Herb. 17: 173. 1913.

Rhizome scales (and those at the base of the petiole) with a long portion, one cell wide, below the spherical terminal cell; leaf usually ca. 0.4-1 m. long, its axes glabrous or thinly ceraceous or thinly pubescent, petiole and the rachis deep reddish brown to blackish; lamina long-triangular to deltoid, pinnate-pinnatifid to tripinnate, pinnae inequilateral, those on the basiscopic side better developed, pinnules at nearly right angles to the pinna-rachis, the lower surface usually white, pale yellow or bright yellow ceraceous, or pubescent.

The following key is supplementary to the headings in the key to species. It may be useful for the identification of certain material that is not typical of either *P. calomelanos* nor *P. tartarea*.



FIGS. 37-42. Fig. 37. *Pterozonium reniforme:* fertile plant, × ½, Peru, *Spruce 4641*, GH. Fig. 38. *Pityrogramma calomelanos* var. *calomelanos:* pinna, × ½, Peru, *Mexia 6101*, GH. Fig. 39. *P. calomelanos* var. *ochracea:* A, pinna, × 1, Peru, *Mexia 8166*, GH; B, section of petiole, enlarged, Peru, *Tryon & Tryon 5366*, GH. Fig. 40. *P. tartarea* var. *tartarea:* A, central pinnae of small leaf, × ½, Peru, *Tryon & Tryon 5429*, GH; B, apex, basal pinna of large leaf, × ½, Colombia, *Schiefer 610*, GH. Fig. 41. *P. chrysoconia:* central pinnae, × ½, Colombia, *H. H. Smith 1061*, GH. Fig. 42. *P. ferruginea:* A, central pinnae, × ½, Peru, *Tryon & Tryon 5451*, GH; B, section of petiole, enlarged, *idem;* C, spores, three views, enlarged, *idem.*

Lamina lanceolate to ovate-lanceolate, or in large leaves long-triangular, its apex often more or less acute or abruptly acuminate; apical pinnae strongly ascending; pinnules acute, serrate, or acutely pinnatifid; basal inferior pinnules more strongly ascending on the upper than on the lower pinnae. .... *P. calomelanos*

Lamina long-triangular, to deltoid in large leaves, its apex evenly long-acuminate; apical pinnae nearly or quite at right angles to the rachis; pinnules obtusely lobed or pinnatifid; basal inferior pinnules at about the same angle to the pinna-rachis on all pinnae (or in large leaves the basal inferior tertiary segments so in relation to the pinnule-rachis). .... *P. tartarea*

2a. **Pityrogramma tartarea** var. **tartarea.** FIG. 40, MAP 10.

Acrostichum tartareum Cav. Descr. 242. 1802. Type: near Guamantanga, Peru, *Née*, seen by C. Chr. at MA (Dansk Bot. Ark. 9(3): 10. 1937).

Gymnogramma peruviana Desv. Ges. Naturf. Freunde Berl. Mag. 5: 329. 1811. Type: Peru, *Jos. de Jussieu* (Herb. Jussieu no. 1009) P! photo GH.

Pityrogramma peruviana (Desv.) Maxon, Contrib. U. S. Nat. Herb. 17: 173. 1913.

Pityrogramma calomelanos var. *peruviana* (Desv.) Farw. Am. Midl. Nat. 12: 280. 1931.

Lamina ceraceous beneath, the wax white to pale (cream) yellow, rarely very sparse and almost colorless; rarely partly ceraceous-pubescent.

Greater Antilles; Mexico to Panama; Venezuela, Colombia, Ecuador and Galápagos Islands south to Bolivia; Brazil.

Rocky and shrubby hillsides, in crevices of rocks and Inca walls, on shrubby slopes and on cliffs, Piura to Puno, 800-4000 m.

Selected specimens: PIURA: arriba de Canchaque, *Ferreyra 3106* (GH, USM); Prov. Piura, *N. Angulo 2168* (GH). LAMBAYEQUE: 29 km. from Olmos, on road to Jaén, *Correll & Smith P803* (GH). CAJAMARCA: Macash, prov. Celendín, *Ridoutt 507* (GH). AMAZONAS: between Donilas and Cohechan, *Soukup 4132* (F); Pomacocha, prov. Chachapoyas, *López et al. 4394* (GH). LIBERTAD: Retamas, prov. Pataz, *López & Sagástegui 3604* (GH). HUANUCO: Mito, *Macbride & Featherstone 1429* (F, US), *Bryan 380* (F); Carpish, *Coronado 60* (GH, UC), *87* (UC); Hacienda Paty, prov. Huánuco, *Ferreyra 9415* (GH, USM). JUNIN: Carpapata, prov. Tarma, *Soukup 3476* (F, GH), *Cerrate 2776* (GH, USM); Huacapistana, *Ferreyra 11245* (GH, USM), *Coronado 273* (UC), *Tryon & Tryon 5429* (BM, F, GH, U, UC, USM); Palca, *Correll & Smith P763* (GH). CUZCO: Machu-Picchu, *Ferreyra 9913* (GH, USM), *Coronado 108* (GH, UC), *Mexia 8086* (F, GH, US); Torontoy, *Herrera 1598* (US);

Maps 9-12. Map 9, *Pityrogramma calomelanos* var. *ochracea*. Map 10, *P. tartarea* var. *tartarea*. Map 11, *P. ferruginea*. Map 12, *P. trifoliata*.

Valle de Cosñipata, *Scolnik 883* (US); Toccorochayoc, prov. Paucartambo, *Woytkowski 95* (GH, USM). PUNO: near Puno, *Soukup 450* (F).

2b. **Pityrogramma tartarea** var. **aurata** (Moore) Tryon, Contrib. Gray Herb. 189: 65. 1962.

Gymnogramma tartarea var. *aurata* Moore, Gard. Chron. 1870: 493. Type: Cultivated by Veitch from a collection by Pearce in Peru. (The specimen of *Pearce 218* at K! photo GH, and Domin, Rospr. II. Tr. Ceské Akad. 38(4): t. 1. 1929, may be the type as Domin says; it does clearly represent Moore's name).

Pityrogramma Presliana Domin, Publ. Fac. Sci. Univ. Charles 88:6. 1928. Type: Peru, *Matthews 1823*, K! photo GH.

Lamina ceraceous beneath, the wax bright yellow.

Colombia, Ecuador and Galápagos Islands to Argentina. Open places, clay banks and among rocks, southwest Loreto to Cuzco, 800-1800 m.

Specimens seen: LORETO: Divisoria, *Ferreyra 1668* (GH, USM). HUANUCO: near Pozuzo, *Macbride 4793* (F, US); Villcabamba, Río Chinchao, *Macbride 4995* (F, GH, US). JUNIN: Chanchamayo valley, *Schunke 28* (F, US); near San Ramón, *Schunke A177* (US); between Huacapistana and San Ramón, *Coronado 259* (GH, UC). CUZCO: Tanamayo, prov. Paucartambo, *Vargas 6479* (UC).

2c. **Pityrogramma tartarea** var. **Jamesonii** (Baker) Tryon, Contrib. Gray Herb. 189: 66. 1962.

Lamina pubescent beneath, not ceraceous.

Colombia and Ecuador; this variety may be expected to occur in Peru in the northern Andes adjacent to Ecuador.

3. **Pityrogramma chrysoconia** (Desv.) Domin, Publ. Fac. Sci. Univ. Charles 88:10. 1928. FIG. 41.

Acrostichum chrysoconium Desv. Mém. Soc. Linn. Paris 6: 212. 1827. Type: Peru, evidently *Dombey*, P, photo GH; isotype: B! photo GH, fragment US!

Gymnogramma Ornithopteris Kl. Linnaea 20: 413. 1847. Type: Venezuela, *Moritz 288*, B! photo GH, fragment US!; isotype: K! photo GH.

Pityrogramma Ornithopteris (Kl.) Knuth, Fedde Rep. Beih. 43: 95. 1926.

Rhizome scales (and those at the base of the petiole) with only a short portion, one cell wide, below the spherical terminal cell; leaf ca. 25-80 cm. long, its axes glabrous or thinly ceraceous, petiole (at least the upper portion) and the rachis straw-colored to light brown; lamina long-triangular, bipinnate to bipinnate-pinnatifid, pinnae inequilateral, those on the basiscopic side somewhat better developed, pinnules nearly at right-angles to the pinna-rachis, the lower surface white or yellow ceraceous.

Plants with white wax on the leaves and those with yellow wax both occur nearly throughout the range of the species and there seems to be no reason to recognize these variants.

Costa Rica to Panama; Jamaica; British Guiana to Colombia, south to Bolivia.

Rocky and shrubby slopes and hillsides and Inca walls, Huánuco to Cuzco, 2000-2800 m.

Specimens seen: HUANUCO: Mito, *Macbride & Featherstone 1393* (F, US), *Bryan 182* (F); Mitotambo, arriba de Mito, *Ferreyra 10348* (GH, USM). HUANCAVELICA: Chuspi, Tocas, *Tovar 2052* (GH, USM). CUZCO: Huadquiña, *Bües 1319* (US); Valle de Occobamba, *Bües 851* (US); Santa Rita, prov. Urubamba, *Vargas 2683* (US); Valle de Amparaes, prov. Paucartambo, *Bües 1836* (US).

4. **Pityrogramma ferruginea** (Kze.) Maxon, Contrib. U. S. Nat. Herb. 17: 173. 1913. FIG. 42, MAP 11.

Gymnogramma ferruginea Kze. Linnaea 9: 34. 1834. Type: Quebrada de Chinchao, Peru, Jul. 1829, *Poeppig, Diar. 1160;* isotype: P! photo GH.

Eriosorus Ruizianus Fée, Gen. Fil. 152, t. 13, f. 2. 1852. Type: Peru, *Ruiz.*

Rhizome scales (and those at the base of the petiole) with a rather long portion, one cell wide, below the long-conical terminal cell; leaf ca. 0.25-1 m. long, its axes densely and persistently lanate (the petiole sometimes deciduously so), petiole and rachis atropurpureous or blackish; lamina narrowly elliptic, pinnate-pinnatifid to pinnate-pinnatisect, pinnae equilateral, the pinnule-lobes usually somewhat ascending, the lower surface densely, to rarely thinly, lanate.

The dense lanate covering of the whole leaf makes this a most distinctive species. It is the only species in the genus with a markedly disjunct range. A hybrid of *P. ferruginea* and *P. trifoliata* is treated under the latter species.

Guatemala to Panama; Peru.

Moist and dry cliffs, rocky banks, crevices of rocks, Huánuco to Ayacucho, 750-1800 m.

Specimens seen: HUANUCO: Río Huallaga cañon, below Santo Domingo, *Macbride 4261* (F, US); 25 km. toward Lima from Tingo María, *Allard 21530* (GH, US), *21531* (US). PASCO: Oxapampa, *Soukup 1822* (F, US), *3351* (F, GH). JUNIN: east of La Merced, *Hutchison 1205* (GH, UC); Dos de Mayo, *Killip & Smith 25845* (F, GH, US); cerca de San Ramón, *Cerrate 2865* (GH, USM), *Tovar 2234* (GH, USM); 8 km. sw. of San Ramón, *Tryon & Tryon 5451* (BM, F, GH, U, UC, US, USM); vicinity of San Ramón, *Constance & Tovar 2233* (UC). AYACUCHO: Ccarrapa, between Huanta and Río Apurímac, *Killip & Smith 22482* (US).

5. **Pityrogramma trifoliata** (L.) Tryon, Contrib. Gray Herb. 189:68. 1962. FIG. 43, MAP 12.

Acrostichum trifoliatum L. Sp. Pl. 2: 1070. 1753. LINN sheet 1245.9, photo A, and Sloane, Hist. Jam. t. 45, f. 2, are both this species.

Trismeria aurea Fée Mém. Fam. Foug. 5 (Gen. Fil.): 165. 1852. *(nom. superfl. illegit. = Acrostichum trifoliatum* L.*)*

Trismeria microphylla Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 165. 1852, ex char. "Peruvia".

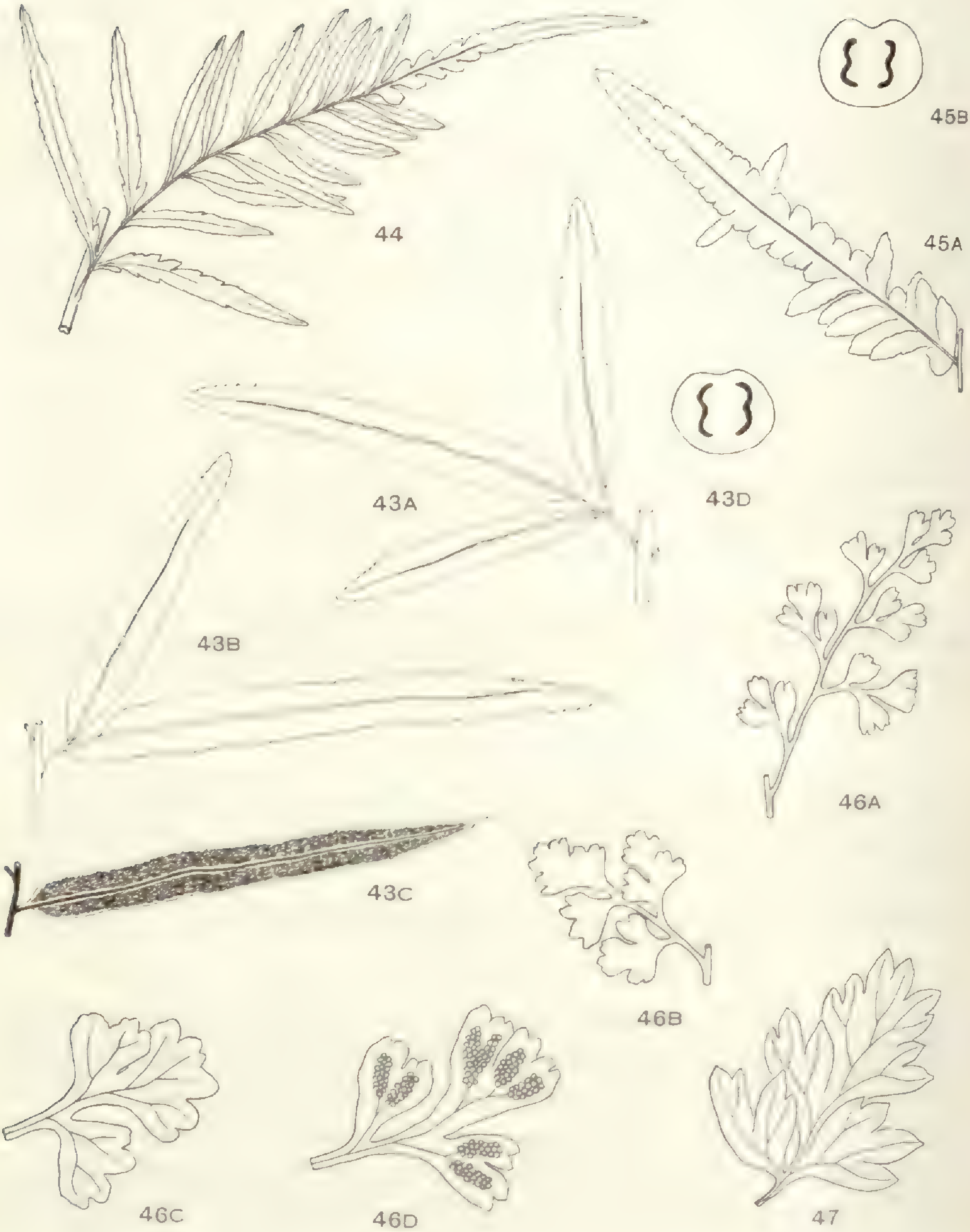
Trismeria trifoliata (L.) Diels, Nat. Pflanz. 1(4):265. 1899.

Rhizome scales (and those at the base of the petiole) with a moderately long portion, one cell wide, below the long-conical to enlarged terminal cell; leaf ca. 0.5-1.25 m. long, its axes glabrous to thinly ceraceous, petiole and rachis light reddish brown to blackish; lamina narrowly lanceolate to usually elongate, 1-pinnate to bipinnate, pinnae equilateral or inequilateral, pinnules (when present) ascending, the lower surface of the pinnae glabrous to usually white or yellow ceraceous.

Pityrogramma trifoliata usually has somewhat dimorphic leaves, the fertile ones being taller and more erect than the sterile. In this species and its hybrids the two vascular bundles in the petiole (about 1/3 the distance to the lamina) are C-shaped with the back of the C curved forward. In the other species the vascular bundles are roundish, oval or C-shaped. The pinnae of *P. trifoliata* are usually simple, bifoliolate or trifoliolate, rarely to 7-foliolate. The hybrids with *P. calomelanos* and *P. ferruginea* differ in having the pinnae with many segments.

Southern Florida; Greater Antilles; Mexico to Costa Rica (notably absent from Panama); Venezuela to Colombia south to Bolivia, Argentina and Chile (Arica); Paraguay, Uruguay and Brazil.

Open rocky ground, or in gravel, along road borders, river banks, irrigation ditches, etc., Piura to Loreto, south to Cuzco and Arequipa, 150-2200 m.



FIGS. 43-47. **Fig. 43.** ***Pityrogramma trifoliata:*** **A, B, sterile pinnae, × ½.** Costa Rica, *Skutch 2295*, GH; C, fertile pinna, × ½, *idem;* D, petiole section, enlarged, *idem.* Fig. 44. *P. calomelanos* var. *ochracea* × *trifoliata:* sterile pinna, × ½, Peru, *Tryon & Tryon 5440*, GH. Fig. 45. *P. ferruginea* × *trifoliata:* A, sterile pinna, × ½, Peru, *Tryon & Tryon 5449*, GH; B, petiole section, enlarged, *idem.* Fig. 46. *Anogramma leptophylla:* A, sterile pinna, × 1, Peru, *Mexia 8083*, GH; B, sterile pinna, × 1, Peru, *Tryon & Tryon 5416*, GH; C, sterile ultimate segments, × 2½, *idem;* D, fertile ultimate segments, × 2½, Peru, *Mexia 8083*, GH. Fig. 47. *A. chaerophylla:* sterile pinnule, × 2½, Brazil, *L. B. Smith 1202*, GH.

Selected specimens: PIURA: Serrán to Canchaque, *Ferreyra 10782* (USM). LAMBAYEQUE: 20 km. from Olmos, on road to Jaén, *Correll & Smith P796* (GH). CAJAMARCA: South of Ichocán, on road to Cajabamba, *Correll & Smith P913* (GH); alrededores de San Benito, prov. Contumazá, *Sagástegui 3740* (GH). SAN MARTIN: Tarapoto, *Spruce 4158* (BM, GH, US). LORETO: lower Río Huallaga, *L. Williams 4640* (F); Boquerón de Abad, *Ferreyra 1109* (USM). LIBERTAD: Trujillo, *Osgood & Anderson 28* (F), *29, 30* (F, US), *Worth et al. 8887* (GH, UC). HUANUCO: Huánuco to Muña, *Mexia 4100* (GH, MO, UC, US); Huánuco, *Macbride & Featherstone 2066* (F, US); Muña, *Macbride 4051* (F, US); Tingo María, *Soukup 2191* (F), *Allard 22051* (US). LIMA: Santa Eulalia, *Coronado 1* (GH, MO, UC, US); Huaral, *Saunders 154* (BM), Chosica, *Macbride 2856* (F, GH, MO, US), *Tryon & Tryon 5342* (BM, F, GH, MO, NY, U, UC, US, USM); Sayán, *Ferreyra 3505* (BM, USM). JUNIN: La Merced, *Killip & Smith 23496* (F, US), *Soukup 1095, 1107* (F); Chanchamayo valley, *Schunke 1377* (F). AYACUCHO: Ayna, *Killip & Smith 23112* (US). APURIMAC: 45 km. from Abancay, on road to Challhuanca, *Saunders 764* (GH); Kairanka, prov. Grau, *Vargas 5868* (UC). CUZCO: Sisal to Cunyacc, prov. Anta, *Vargas 7411* (MO, UC); San Miguel, *Cook & Gilbert 1087* (US). AREQUIPA: Huario, below Chuquibamba, *D. Stafford 1149* (BM); Majes valley, north of Arequipa, *D. Stafford 1191* (BM).

5a. **Pityrogramma calomelanos** var. **ochracea** × **trifoliata.** FIG. 44.

Gymnogramma Herzogii Rosenst. Med. Rijks Herb. 19: 21. 1913. Type: Bolivia, *Herzog 2000;* isotype: US!

Petiole and rachis thinly pubescent to glabrous, segments pubescent beneath.

Peru and Bolivia.

Dry, rocky stream bed, Junín, 750 m. and Cuzco, 1200 m.

Specimens seen: JUNIN: La Merced, *Tryon & Tryon 5440* (GH). CUZCO: Puente Chaupemayo, sobre el Río Sambray, *Büés 1936* (US).

5b. **Pityrogramma ferruginea** × **trifoliata.** FIG. 45.

Petiole and rachis closely and densely lanate, although deciduously so.

The only collection has the pinnules markedly irregular in their length.

Peru.

Exposed crevices of rocks, Junín, 1000 m.

Specimens seen: JUNIN: 10 km. sw. of San Ramón, *Tryon & Tryon 5449* (BM, GH, U, US).

6. **Pityrogramma Pearcei** (Moore) Domin, Publ. Fac. Sci. Univ. Charles 88:9. 1928.

Gymnogramma Pearcei Moore, Gard. Chron. 1864: 340. Type: "Cult. Veitch ex Pearce"; two specimens, *Pearce 274* and "*Gymnogramma Pearcei*, n. sp." K! photos GH, are authentic.

Lamina long-triangular, quadripinnate with slender ultimate lobes, pinnae equilateral.

The original material of this species was probably collected in Peru. It has not been gathered again and its status is uncertain. It may represent a valid species or it may be a highly dissected leaf-variant of another species.

Specimens seen: "Chile," *Pearce* (K); "Eastern Andes," *Pearce 274* (K); Hort. Veitch. in 1889 (K).

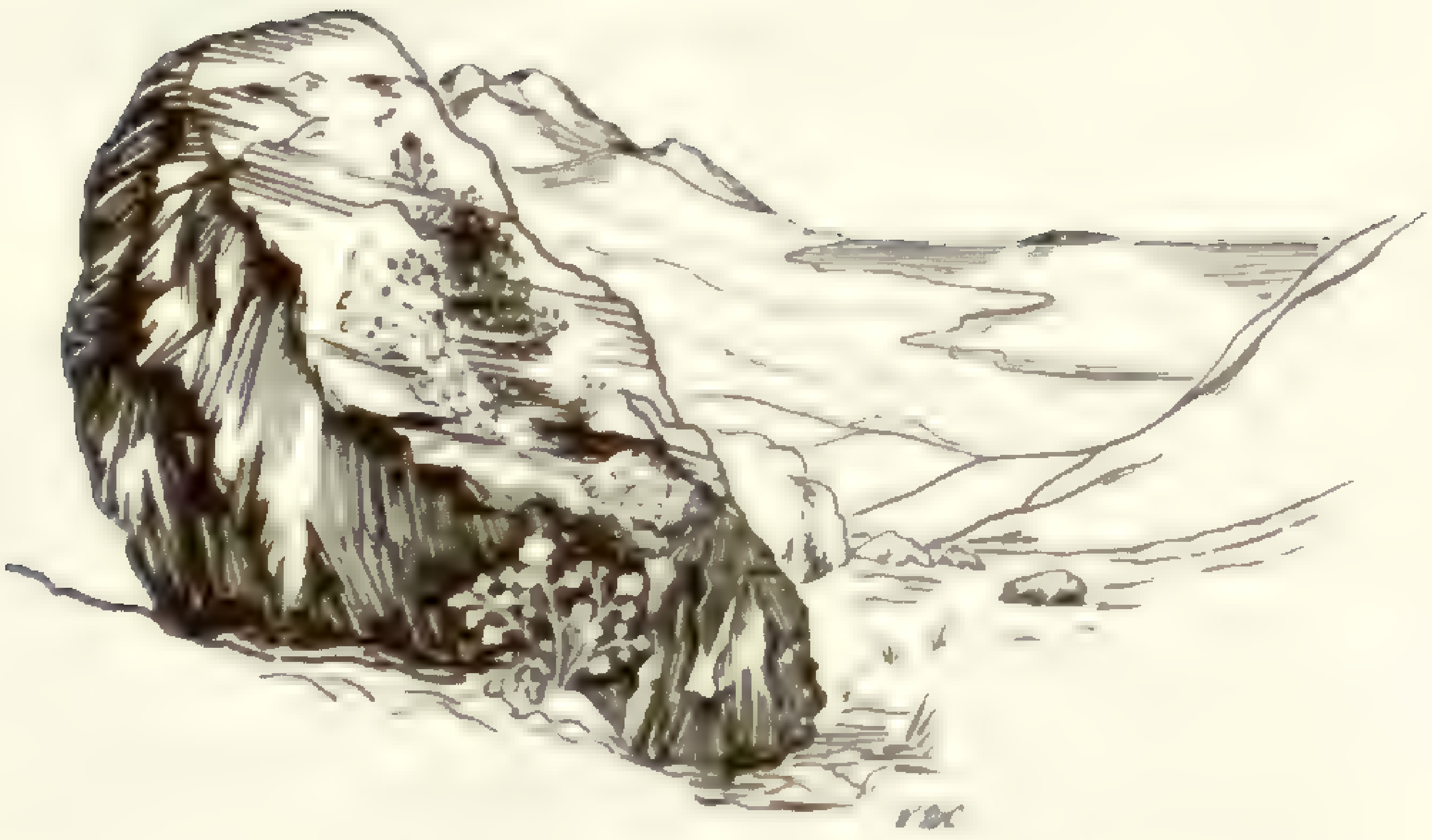


FIG. 48. *Anogramma leptophylla*, Loma Lachay (Lima).

10. ANOGRAMMA Link, Fil. Sp. Cult. 137. 1841. Type: *Polypodium leptophyllum* L. = *Anogramma leptophylla* (L.) Link. FIG. 48.

Terrestrial, the rhizome erect, small to minute, with a few thin scales (or also similar trichomes), bearing the leaves in a cluster; leaves very small to medium sized, bipinnate to quadripinnate, glabrous, veins free; sporangia borne along the veins back of the unmodified margin, often confluent over the segment at maturity, indusium and paraphyses absent. — 5 species in America.

Domin, K. Generis Pityrogramma (Link) species ac sectiones in clavem analyticam dispositae (4. Anogramma), Publ. Fac. Sci. Univ. Charles no. 88: 9. 1928.

Tryon, R. Anogramma, *in* Tax. Fern Notes, II, Contrib. Gray Herb. 189: 74-76. 1962.

The sporophyte is annual; it grows rather rapidly and lives for only a single season. The gametophyte is said to be perennial, producing buds which survive an adverse season and produce new sporophytes the following year. The longevity of both the sporophyte and gametophyte of the different species needs to be confirmed in nature. *Anogramma* represents a reduced and specialized evolutionary development closely related to *Pityrogramma.*

There is a single species in Peru but another, *Anogramma chaerophylla,* grows in Bolivia and may eventually be found in Peru.

KEY TO SPECIES

Ultimate lobes obtuse, 2-veined, bifid lobes frequent, pinnules obovate-cuneate. .... *A. leptophylla*

Ultimate lobes acute, mostly 1-veined, pinnules ovate to ovate-lanceolate. .... *A. chaerophylla* (Desv.) Link, Fig. 47.

Anogramma leptophylla (L.) Link, Fil. Sp. 137. 1841. FIGS. 46, 48. *Polypodium leptophyllum* L. Sp. Pl. 2: 1092. 1753. Syntypes: Magn. Monsp. 5, t. 5; Barr. Rar. 1270, t. 431; LINN 1251.56, photo A.

Leaves ca. 5-15 cm. long, the petiole long, light brown to straw-colored near the apex, to dark reddish-brown at the base; lamina herbaceous, lanceolate, ovate or deltoid, pinnules obovate-cuneate, the ultimate lobes obtuse, often bifid and with two veins.

This species is known only from some of the lomas of the Department of Lima and from Machu-Picchu. At Loma de

Lachay it grows under the edges of large rocks and is well hidden from the casual collector.

Mexico and Central America; Ecuador and Peru; Old World.

Among rocks, under boulders, on Inca walls, Lima and Cuzco, 500-2400 m.

Specimens seen: LIMA: Loma de Lachay, *Coronado 14* (GH, UC, US), *Tryon & Tryon 5416* (BM, F, GH, U, US, USM); Loma de Quilmaná, *Coronado 26* (GH, UC, US); Loma de Granados, 12 km. n. of Huaral, *Stork & Vargas 9333* (GH, UC). CUZCO: Machu-Picchu, *Mexia 8083* (F, GH, UC), *Coronado 94* (GH, UC, US); Machu-Picchu Station, *Vargas 2591* (US).

11. GYMNOPTERIS Bernh. Jour. Bot. Schrad. 1(2):297. 1799. Type: *Acrostichum rufum* L. (not *Pteris ruffa* L. as often stated) = *Gymnopteris rufa* (L.) Underw.

Terrestrial, the rhizome rather small, erect or nearly so, scaly, bearing the leaves in a cluster; leaves small or medium sized, 1-pinnate or bipinnate, pubescent, veins free; sporangia borne along the veins for most of their length, slightly back of the unmodified margin, indusium and paraphyses absent. — 4 American species.

A few specimens seem somewhat intermediate between the two well marked extremes of the Peruvian species. A critical study of all of the American material of these species is needed in order to understand their relation to each other.

KEY TO SPECIES

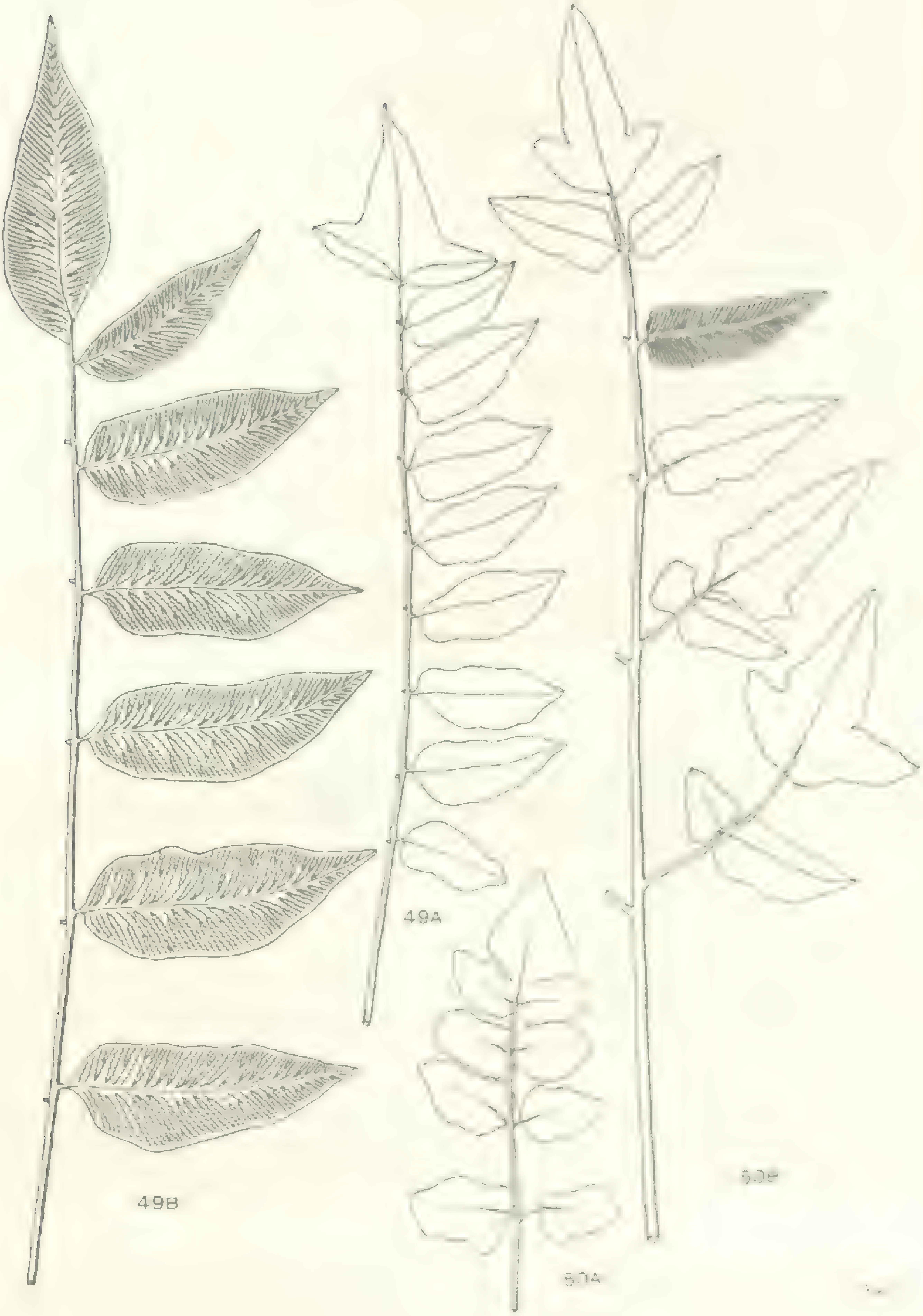
All pinnae short-stalked, the dark color of the stalk ending abruptly at the usually cuneate (to subcordate) base, basal pinnae slightly smaller than those above, pinnae entire. .... 1. *G. rufa*

Lower pinnae with (often long) stalks, longer than the upper ones, the dark color of the stalk entering the usually cordate (to broadly cuneate) base, the basal pinnae larger than those above, pinnae entire, lobed or 1-pinnate. .... 2. *G. tomentosa*

1. **Gymnopteris rufa** (L.) Underw. Bull. Torrey Cl. 29: 627. 1902. FIG. 49.

Acrostichum rufum L. Syst. Nat. ed. 10, 1320, 1759. Type: Sloane, t. 45, f. 1. (Not *Pteris ruffa* L. Sp. Pl. 2: 1074. 1753 which is maintained in Syst. Nat. 1321). Bernhardi did not transfer this species to *Gymnopteris*, as often cited; Underwood did, although he may not have been the first one to do so.

Leaves ca. 20-60 cm. long, petiole usually long, it and the rachis dark reddish-brown to atropurpureous, pubescent with short, acicular tri-



FIGS. 49-50. Fig. 49. *Gymnopteris rufa:* A, sterile lamina, × ½, Venezuela, *Fendler 302*, GH; B, fertile lamina, × ½, *idem*. Fig. 50. *G. tomentosa:* A, sterile lamina, × ½, Peru, *Tryon & Tryon 5374*, GH; B, fertile lamina, × ½, Peru, *Vargas* [illegible], GH.

chomes and fewer, long, multicellular ones; lamina narrowly elliptic to lanceolate, 1-pinnate, the pinnae entire, usually cuneate (to subcordate), short-stalked, the dark color of the stalk not continued into the pinna, both surfaces more or less pubescent with acicular, multicellular, more or less appressed, trichomes.

Southern Mexico to Panama; Greater Antilles; Surinam to Colombia, south to Peru.

In forest, San Martín, 400-800 m.

Specimens seen: SAN MARTIN: Juan Jui, *Klug 4174* (F, GH, UC).

2. **Gymnopteris tomentosa** (Lam.) Underw. Bull. Torrey Cl. 29: 627. 1902. FIG. 50.

Asplenium tomentosum Lam. Encycl. 2: 308. 1786. Syntypes: Brazil, *Commerson, Dombey.* A sheet in Herb. Lamarck, P! photo GH, "*Asplenium tomentosum* e Brasilia" (without collector) is this species.

Leaves ca. 20-75 cm. long, petiole long, it and the rachis reddish-brown to atropurpureous, pubescent with short, acicular, trichomes and fewer long, multicellular ones; lamina suboblong to subdeltoid, 1-pinnate and the pinnae entire (or some lobed), usually cordate (to broadly cuneate), or bipinnate, pinnae stalked, the basal ones with longer stalks than those above, both surfaces more or less pubescent with acicular, multicellular, more or less appressed trichomes.

Peru to Argentina, Paraguay and Brazil.

Forest slopes, stony clearings and in woods, San Martín to Cuzco, 700-1600 m.

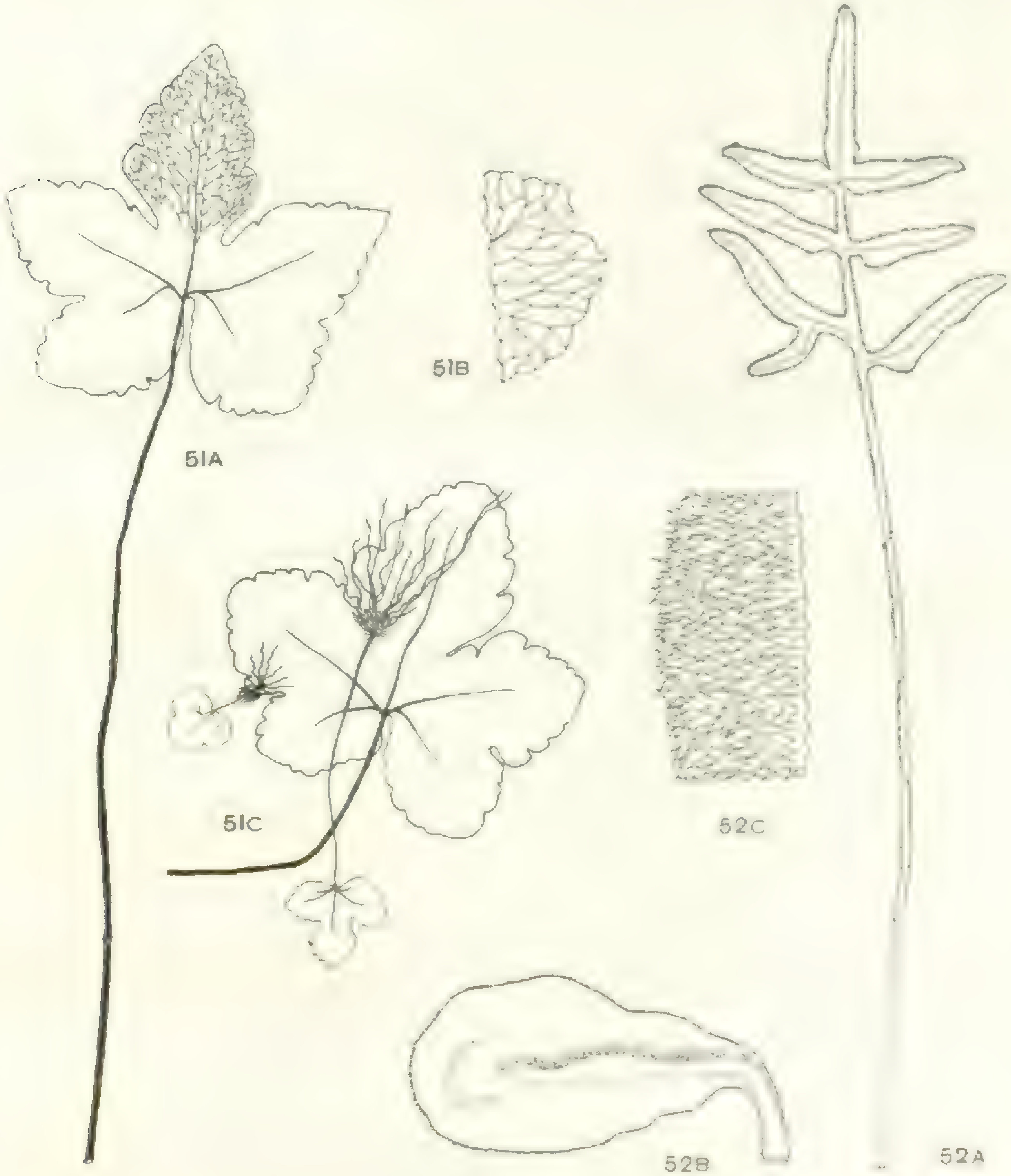
Selected specimens: SAN MARTIN: Tarapoto, *Spruce 3992* (B, GH), *Woytkowski 35228* (UC), *L. Williams 5484* (F). HUANUCO: near Pozuzo, *Macbride 4788* (F, US). JUNIN: La Merced, *Macbride 5303* (F); Río Paucartambo, near Perené Bridge, *Killip & Smith 25345* (US); Río Pinedo, n. of La Merced, *Killip & Smith 23592* (GH, US). CUZCO: Quellauno, prov. Convención, *Vargas 13557* (GH); Quillabamba, *Coronado 122* (GH, UC, US); Santa Ana, *Cook & Gilbert 1537* (GH, US), *1690* (US); Santa Rosa, Urubamba valley, *Cook & Gilbert 1724* (US); Torontoy, *Herrera 1331* (US); Potrero, 8 km. w. of Quillabamba, *Tryon & Tryon 5374* (GH, U, US, USM).

12. HEMIONITIS L. Sp. Pl. 2: 1077. 1753; Gen. Pl. 485. 1754. Type: *Hemionitis palmata* L.

Terrestrial, the rhizome small, erect or nearly so, scaly, bearing the leaves in a cluster; leaves small, pedately lobed, pubescent, veins anastomosing; sporangia borne all along the veins, nearly to the unmodified margin, indusium and paraphyses absent. — 5 American species.

Hemionitis palmata L. Sp. Pl. 2: 1077. 1753. Type: LINN 1248.3, photo A, is this species. Fig. 51.

Sterile leaves ca. 3-10 cm. long, 3-lobed or pedately 5-lobed, clustered at the base of the few, erect, pedately 5-lobed fertile leaves which are ca. 10-25 cm. long; principal lobes shallowly lobed or crenate on the margin, tawny to rufous pubescent with multicellular, slender-tipped trichomes, these especially evident along the margins, the brown to dark brown petiole with similar trichomes.



Figs. 51-52. Fig. 51. *Hemionitis palmata:* A. fertile leaf, × ½, Guatemala, *Deam 460*, GH; B. portion of sterile segment, × 1, *idem;* C. sterile leaf with young plants, × ½, Mexico, *Dressler & Jones 76*, GH. Fig. 52. *Trachypteris pinnata:* A. fertile leaf, × ½, Argentina, *Schreiter 8876*, GH; B. sterile leaf, × ½, *idem;* C. lower surface of sterile leaf, × 2½, *idem.*

This is a most attractive species, the sporangia exactly tracing the pattern of the veins. It has been cultivated at Iquitos: *Williams 3559* (F).

West Indies; Mexico and Central America; Guianas to Colombia, south to Peru and Bolivia; Brazil.

In forests, San Martín and Cuzco, 500-900 m.

Specimens seen: SAN MARTIN: Tarapoto, *Spruce 3993* (GH, US); Juan Jui, alto Río Huallaga, *Klug 4288* (F, GH, MO, UC, US, USM); near Tarapoto, *L. Williams 6793* (F, US). CUZCO: Santa Ana, *Cook & Gilbert 1477* (US).

13. TRACHYPTERIS Christ, Denkschr. Schweiz. Naturfors. Gesells. 36: (Monogr. Elaph.) 150. 1899. Type: *Acrostichum aureonitens* Hook.= *Trachypteris aureonitens* (Hook.) Christ = *Trachypteris pinnata* (Hook. f.) C. Chr.

Terrestrial, the rhizome rather small, erect or decumbent, scaly, bearing the sterile leaves in a rosette, the few fertile ones in a cluster; leaves small, the sterile with the lamina entire, the fertile with the lamina deeply pinnatifid to 1-pinnate, densely scaly beneath, glabrate above, veins anastomosing; sporangia borne all along the veins nearly to the unmodified margin, indusium and paraphyses absent. — 1 American species.

Trachypteris pinnata (Hook. f.) C. Chr. Ind. Fil. 634. 1906. FIG. 52.

Hemionitis pinnata Hook. f. Trans. Linn. Soc. 20: 167. 1847. Type: Charles Isl., Galápagos Isls., *Darwin.*

Acrostichum aureonitens Hook. Ic. Pl. t. 933 (Cent. Ferns t. 33). 1854. Type: Galápagos Isls., *Cuming 109* (the plate was drawn from this specimen) K! photo GH.

Acrostichum Gillianum Bak. Jour. Bot. 1882: 310. Type: Arassnahy, Minas Gerais, Brazil, *Gille* (*Glaziou* no. *13341*) K! photo GH; isotype: BM!

Sterile leaves several, ca. 5-8 cm. long, more or less prostrate, spathulate to obovate, sessile or nearly so, rarely with a few lobes, scales on the lower surface brownish, appressed, imbricate, more or less dentate; fertile leaves few, ca. 12-25 cm. long, erect, subdeltoid to short-oblong, with a long, brown to dark reddish-brown, deciduously scaly petiole, scales on the lower surface similar to those of the sterile leaf.

A critical study of the American material may show that two or three species, or geographic varieties of one species, are present.

Galápagos Islands; Peru, Bolivia, Argentina and Brazil.

In rocky woods and in forest, Cajamarca, San Martín and Cuzco, 850-2750 m.

Specimens seen: CAJAMARCA: Jaén, *Rauh P2160* (B); Río Chamaya, Olmos to Río Marañon, prov. Jaén *Hutchison 1424* (F, GH, UC). SAN MARTIN: Tambo de Carrizal, *Stübel 1016* (B). CUZCO: Santa Ana, *Cook & Gilbert 1480* (US); Huadquiña, *Bües 1339* (US); Sahuayacu, *Bües 837* (US).

14. **CERATOPTERIS** Brongn. Bull. Soc. Philomath. Paris 1821: 186. Type: *Acrostichum thalictroides* L. = *Ceratopteris thalictroides* (L.) Brongn.

Aquatic (floating on water or rooting in mud), the stem small, erect, with a few scales, bearing the sterile leaves in a rosette, the fertile ones in a cluster; leaves small to medium sized, the sterile lobed to bipinnate-lobed, the fertile 1-pinnate to quadripinnate, glabrous, veins anastomosing; sporangia borne sparingly along the marginal commissure, sometimes also on the lateral veins, more or less covered by an indusium formed from the reflexed, somewhat modified margin, paraphyses absent. — 4 species in America.

Benedict, R. C. The genus Ceratopteris: a preliminary revision, Bull. Torrey Cl. 36: 463-476. 1909.

Benedict, R. C. Ceratopteridaceae, N. Amer. Fl. 16(1):29-30. 1909.

DeVol, C. E. The geographic distribution of Ceratopteris pteridoides, Am. Fern Jour. 67-72. 1957. (The photograph and the map are erroneously labeled *C. thalictroides*).

Ceratopteris pteridoides (Hook.) Hieron. Bot. Jahrb. 34: 561. 1905. FIG. 53.

Parkeria pteridoides Hook. Exot. Fl. 2: t. 147. 1825. Type: District of Essequibo, British Guiana, *Parker;* isotype: GH!

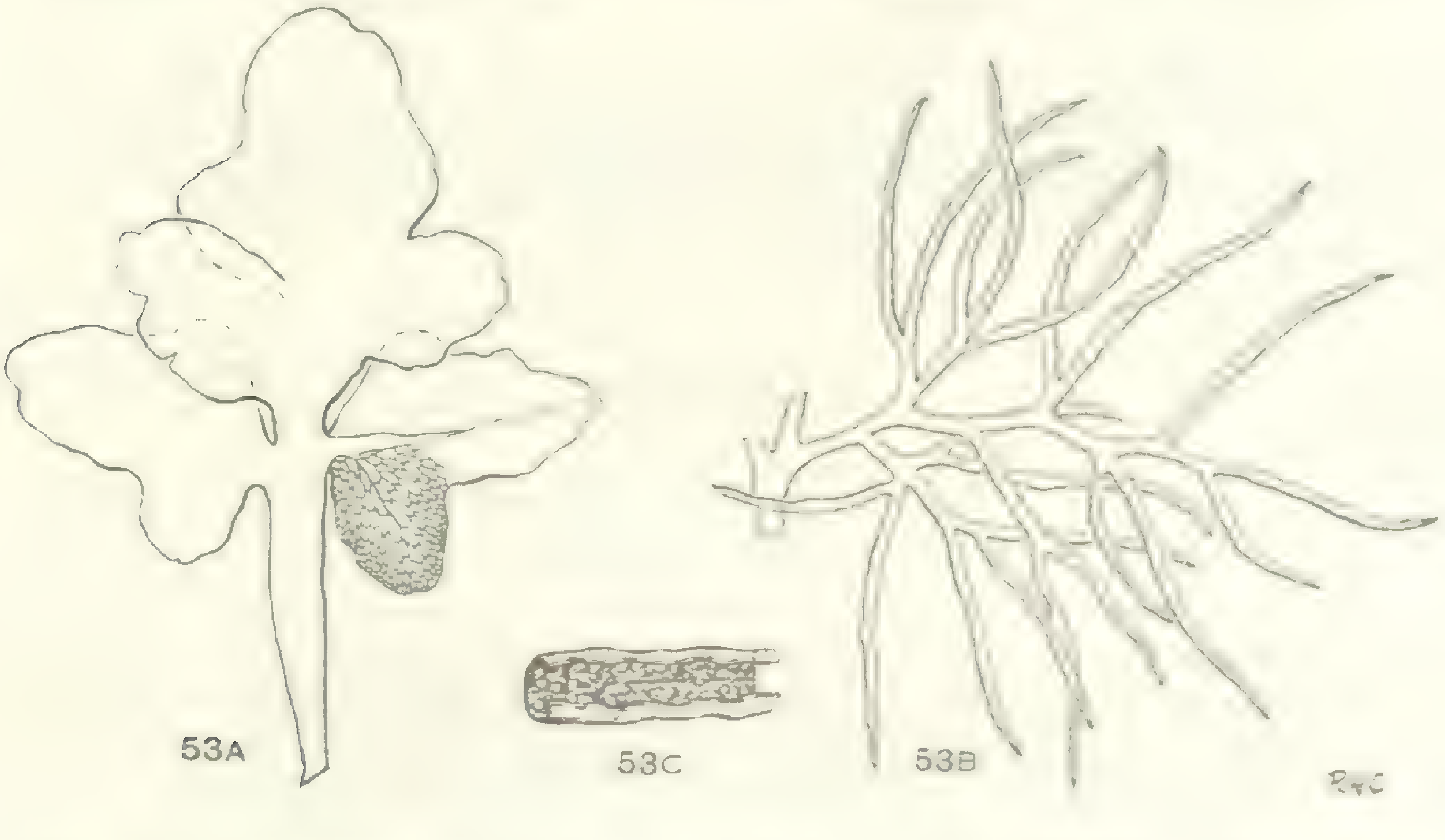


FIG. 53. *Ceratopteris pteridoides:* A, sterile leaf, × ½, Florida, *Curtiss*, GH; B, fertile pinna, × ½, Cuba, *Killip 44595*, GH; C, portion of fertile segment, enlarged, *idem.*

Sterile leaves more or less prostrate, ca. 3-20 cm. long, with a fleshy petiole which is broadest at its apex and narrowed toward the base, or is inflated, lamina deltoid, thin-herbaceous, with broad segments, old leaves often with adventitious buds; fertile leaves more or less erect, ca. 5-35 cm. long, with linear segments; leaves intermediate between the typical sterile and fertile ones are sometimes present.

Southern Florida; Central America; northern South America to Peru, Argentina and Brazil; Old World.

In slow streams and along rivers, Loreto, 100 m.

Specimens seen: LORETO: Río Itaya, Iquitos, *Asplund 14626* (US); Iquitos, *Killip & Smith 27427* (US).

15. CHEILANTHES Sw. Syn. Fil. 5, 126. 1806, conserved name. Type: *Cheilanthes micropteris* Sw.

Adiantopsis Fée, Gen. Fil. 145. 1852. Type: *Adiantum pauperculum* Kze. = *Adiantopsis paupercula* (Kze.) Fée = *Cheilanthes paupercula* (Kze.) Mett.

Terrestrial, the rhizome small to moderately stout, compact to creeping, scaly, bearing the leaves in a cluster or closely spaced; leaves usually small to medium sized, pinnate (pinnate-pinnatifid to quadripinnate), ternate or radiate, glabrous, glandular, ceraceous, pubescent or scaly, veins free; sorus borne on the vein-tips, not paraphysate, marginal, covered by the indusium which is formed from the reflexed, modified margin or (in species 1-3) the strongly revolute margin scarcely modified. — About 35 species in South America.

A genus of 15 species in Peru, these inhabiting sheltered rocky places in the Altiplano and adjacent valleys of the Andes, or some of them growing in exposed situations. *Cheilanthes incarum* and *C. scariosa*, for example, are extreme alpine xerophytes.

KEY TO SPECIES

a. Lamina pubescent or scaly; petiole and rachis terete or rarely the latter grooved on the upper side toward the apex (or in no. 6 most of it grooved). .... b.
  b. Lamina scaly. .... c.
    c. Scales of the rachis predominantly narrowly linear to acicular; ultimate segments suborbicular, minute; rhizome scales with a dark sclerotic central portion and pale thinner margins. .... 1. *C. myriophylla*
    c. Scales of the rachis ovate-acuminate; rhizome scales brownish, concolorous. .... d.

d. Ultimate segments small, suborbicular, their upper surface partially concealed by a persistent pubescence produced from the dissected tips of the scales beneath. .... 2. *C. scariosa*

d. Ultimate segments mostly of moderate size, ovate-deltoid, their upper surface hardly concealed by the deciduous tips of the scales beneath. .... 3. *C. incarum*

b. Lamina pubescent. .... e.

e. Rachis and pinna-rachises pubescent, often becoming glabrous; indusium deeply crenate or lobed; rhizome scales brown to atropurpureous, rigid, shining, with or without very narrow, pale, thinner margins; blade narrowly linear, pinnae mostly alternate, adjacent, very numerous. .... 4. *C. pruinata*

e. Rachis and pinna-rachises pubescent, often becoming glabrous on the under side, the trichomes moderately long (rarely only those of the pinnae so). .... f.

f. Scales at the apex of the rhizome dark brown, rigid, shining, with or without very narrow, pale, thinner margins. .... 5. *C. pilosa*

f. Scales at the apex of the rhizome whitish to light brown, soft, dull, concolorous. .... g.

g. Petioles deciduous, breaking sharply and evenly toward their base; rachis grooved on the upper side or the apical portion alate. .... 6. *C. fractifera*

g. Petioles persistent, finally breaking irregularly; rachis terete or nearly so, not alate. .... h.

h. Pinna-rachis greenish above, the pinna-stalk greenish to blackish; older rhizome scales often with a rigid, dark, sclerotic central portion. .... 7. *C. notholaenoides*

h. Pinna-rachis atropurpureous to blackish above (as is the pinna-stalk) well beyond the basal pinnules or nearly to the tip; older rhizome scales sometimes with a darkened, semi-sclerotic base. .... 8. *C. Moritziana*

a. Lamina glabrous or glandular, or ceraceous-glandular; rachis and usually the petiole grooved on the upper side. .... i.

i. Segments whitish ceraceous-glandular beneath. .... 11. *C. farinosa*

i. Segments glabrous or with scattered non-ceraceous glands beneath. .... j.

j. Lamina ternate to usually radiate. .... 10. *C. radiata*

j. Lamina pinnate. .... k.

k. Indusium confined to the segments. .... l.

l. Rhizome scales bicolorous, with a rather thick, dark center and lighter, thin margins. .... m.

m. Apical part of the petiole, on the upper side, with a light colored, submembranous ridge on each side. .... 9. *C. chlorophylla*

m. Apical part of the petiole, on the upper side, with a rounded ridge on each side, these concolorous with the petiole (or rarely the petiole terete). .... 12. *C. Poeppigiana*

l. Rhizome scales concolorous, wholly brown to atropurpureous, rather thick. .... n.
  n. Apical part of petiole, on the upper side, flat to convex between the small lateral ridges; rhizome erect. .... 13. *C. Orbignyana*
  n. Apical part of petiole, on the upper side, deeply sulcate between the relatively large lateral ridges; rhizome short-creeping, prostrate. .... 14. *C. rufopunctata*
k. Indusium extending onto the segment stalks. .... 15. *C. marginata*

1. **Cheilanthes myriophylla** Desv. Ges. Naturf. Freunde Berl. Mag. 5: 328. 1811. Type: Peru, P! photo GH. Fig. 54, Map 13.

Cheilanthes elegans Desv. Ges. Naturf. Freunde Berl. Mag. 5: 328. 1811. Type: "Chile," P! photo GH, a portion of a pinna, probably from a specimen collected in Peru. *Dombey*, Peru, P! photo GH, det. Desv., may supplement the holotype.

Rhizome moderately stout, short-creeping, multicipital, scales lance-subulate, with a dark sclerotic central portion and paler margins; leaves ca. 15-40 cm. tall, petiole terete, scaly, as is the rachis; lamina lanceolate to lanceolate-oblong or narrowly so, to quadripinnate, pinnae densely scaly beneath, nearly glabrous above, the ultimate segments small, suborbicular; indusium more or less modified, rather continuous.

This species is characterized by its small bead-like ultimate segments that are easily seen on the upper side of the lamina and usually not completely concealed by the scales on the under side. The upper surface of the segments is often slightly pubescent; the narrow scales of the petiole and rachis superficially resemble a mat of hairs. The related *C. lendigera* (Cav.) Sw. differs in having long brownish hairs on the under surface of the segments, a definitely intramarginal indusium and an elongate, slender rhizome with tawny, concolorous scales. C. A. Weatherby (Contrib. Gray Herb. 114: 22. 1936) has discussed the type specimens of Desvaux's two names.

Hispaniola; Mexico to Colombia and Venezuela, south to Bolivia and Argentina; Brazil.

Rocky soil, shrubby hillsides and cliffs, Piura to Puno and Arequipa, 1550-3250 m.

Selected specimens: PIURA: Huancabamba, *Scolnik 1436* (US). CAJAMARCA: Llacanora, *Ferreyra 3218* (USM); entre Cascas y Contumazá, *López et al. 3679* (GH). LIBERTAD: Trujillo to Otusco, *Scolnik 1293* (US); Cerro Chologday, prov. Otuzco, *Sagástegui 77* (GH). ANCASH: Huasta, *Cerrate 2164* (USM); Chiquián, *Cerrate 546* (USM). HUANUCO:

Ambo, *Macbride 3197* (F, US); Acomayo, *Tryon & Tryon 5328* (BM, F, MO, U, US, USM). LIMA: Chancay, e. of Sayán, *Goodspeed 33032* (GH, MO, UC, US); Surco, *Ferreyra 3479* (GH, USM). JUNIN: Palca to Carpapata, *Stork 10958* (F, GH, MO, UC); Vilcabamba, *Tryon & Tryon 5420* (BM, F, GH, MO, U, US, USM). HUANCAVELICA: n. of Pampas, *Stork & Horton 10242* (F, UC). AYACUCHO: Ayacucho, *West 3641* (MO, UC); 45 km. from Nasca on road to Puquio, *Correll & Smith P170* (GH). APURIMAC: Chirhuai, *Vargas 2301* (CUZ); Challhuanca, *Saunders 772* (GH). CUZCO: Cuzco, *Vargas 368* (GH, MO); Anta, *Tryon & Tryon 5363* (BM, F, MO, U, US, USM); PUNO: Sandia, *Weberbauer 724* (B). AREQUIPA: 14 km. n. of Arequipa, *Eyerdam & Beetle 22164* (GH, MO, UC); Arequipa, *Pennell 13184* (F, GH, US).

2. **Cheilanthes scariosa** (Sw.) Presl, Rel. Haenk. 1: 65. 1825. FIG. 55, MAP 14.

Acrostichum scariosum Sw. Syn. Fil. 16. 1806, based on *Acrostichum lanuginosum* Willd. Schrift. Acad. Erfurt, 1802: 31, t. 3, f. 4, not Desf. 1800. Type: Peru, Malaspina Exped. (Herb. Willd. 19554-1), B! photo GH, US.

Cheilanthes ornatissima Maxon, Smiths. Misc. Coll. 65(8):3. 1915. Type: Mountains back of Lima, Peru, *W. E. Safford 996* US!; isotypes: GH! MO! UC!

Cheilanthes tripinnata Copel. Univ. Cal. Publ. Bot. 19: 301, t. 58. 1941. Type: Chincheros to Andahuaylas, Dept. Apurímac, Peru, *West 3724*, UC!

Rhizome rather stout, very short-creeping, multicipital, scales long and filiform, concolorous, light reddish brown; leaves ca. 8-15 cm. tall, petiole densely scaly, terete, as is the rachis; lamina linear to rather narrowly elliptic, tripinnate, pinnae densely scaly beneath, the scales and especially their tips curving over the glabrous upper surface and concealing it, ultimate segments small, subdeltoid; the margin strongly recurved, only very slightly if at all modified into an indusium.

The ultimate segments are small and bead-like as in *C. myriophylla* but they are not easily seen for the under surface is completely concealed, except in age, by the scales, and the upper surface is somewhat concealed by the dissected tips of those scales that extend over the margin. Some of the scales on the rachis have such strongly curved auricles that they give the appearance of a small scale attached to the base. This is one of the most scaly of all ferns and it is perhaps unfortunate that Maxon's appropriate name can not be taken up. C. A. Weatherby (Contrib. Gray Herb. 124: 19. 1939.) has discussed and illustrated the type specimen, and the confusion in the application of the

Maps 13-16. Map 13, *Cheilanthes myriophylla*. Map 14, *C. scariosa*. Map 15, *C. pruinata*. Map 16, *C. pilosa*.

name *C. scariosa* that caused Maxon to redescribe the species.

Peru and Bolivia.

Exposed calcareous rocky places and cliffs, Libertad to Puno, 2700-4300 m.

Selected specimens: LIBERTAD: Yanazara to Huaquil, *López & Sagástegui 3395* (GH). ANCASH: Mahuay, *Cerrate 2200* (USM). LIMA: Matucana, *Macbride & Featherstone 424* (F, US), *Goodspeed 11347* (GH, UC); Río Blanco, *Killip & Smith 21681* (US). JUNIN: Tarma, *Macbride & Featherstone 1049* (F, US); near Tarma, *Tryon & Tryon 5457* (BM, F, GH, MO, U, US, USM); Incahuasi, *Soukup 3170* (BM, F, GH). HUANCAVELICA: se. of Conaica, *Tovar 113* (GH, MO, US); between Colcabamba and Paucarbamba, *Tovar 2087* (GH, USM). APURIMAC: prov. Andahuaylas, *Vargas 8792* (CUZ, UC). CUZCO: vicinity of Cuzco, *Herrera 215* (US); near Cuzco, *Weberbauer* (B); PUNO: Pucará *Weberbauer 425* (B).

3. **Cheilanthes incarum** Maxon, Smiths. Misc. Coll. 65(8):5. 1915. Type: Cuzco, Peru, *Mr. & Mrs. J. N. Rose 19061*, US! FIG. 56.

Rhizome rather stout, short-creeping, multicipital, scales light brown, subulate, attenuate to a capillary tip; leaves ca. 10-25 cm. tall, the petiole densely scaly, terete, as is the rachis; lamina bipinnate to tripinnate, linear-lanceolate, pinnae densely covered with scales beneath, with a few readily deciduous ones above, the ultimate segments mostly ovate-deltoid, their upper surface only partially concealed by the tips of the scales from beneath; indusium rather narrow, more or less continuous.

In general appearance this species is like the previous, *C. scariosa*, and may easily be confused with it. In addition to the characters mentioned in the key, the leaves of *C. incarum* have a definite petiole of 5 cm. or more while those of *C. scariosa* are nearly sessile or have a very short petiole. The lowest pinnae are reduced but not as strongly so as in *C. scariosa* and the rhizome scales are broader, elongate-attenuate and dentate-spinescent. The leaf-cutting is similar to *C. Moritziana* and it may be that this species is a xeric alpine derivative from such a progenitor and not actually related, by its densely scaly leaves, to *C. scariosa*.

Peru and nw. Argentina.

Exposed rocky places, Huancavelica to Cuzco, 2600-3600 m.

Specimens seen: HUANCAVELICA: Mejorada, *Tovar 1014* (GH, USM), *Hutchison 1960* (GH). APURIMAC: 5 km. n. of Huancarama, *West 3903* (UC); Posocoi, prov. Andahuaylas, *Vargas 8792* (UC); 80 km. from Abancay on road to Challhuanca, *Saunders 768* (GH). CUZCO: Cerro Sape, Cuczo, *Ferreyra 2668* (BM, GH, USM); Saxihuaman, *Herrera 212, 2194* (F), *Tryon & Tryon 5343* (BM, F, GH, MO, U, US, USM); Urubamba, *Vargas 7627* (CUZ); near Cuzco, *Herrera 1* (BM, F, UC, US), *Mr. & Mrs. J. N. Rose 19061* (US); near Pisac, *Hunnewell 15860* (GH).

4. **Cheilanthes pruinata** Kaulf. Enum. Fil. 210. 1824. Type: "Peru." FIG. 57, MAP 15.

Cheilanthes digitata Presl, Tent. Pterid. 160. 1836, *nomen nudum*, is perhaps this species; *Dombey*, Peru and *Meyen*, Peru, both at B! are labeled with Presl's name.

Cheilanthes Mathewsii Kze. Farnkr. 1: 50, t. 25. 1840. Type: Peru, *Mathews 605*, BM! photo GH. This specimen, identified by Kunze, may be the holotype, or it may serve to replace the one destroyed at LZ.

Cheilanthes fasciculata Goldm. Nov. Act. Acad. Caes. Leopold.-Carol. Nat. Cur. 19, suppl. 1 (Meyen, Beitr. zur Bot.): 456. 1843. Type: Peru, 9000-12000 ft., *Meyen*, B! photo GH.

Rhizome moderately stout, creeping, multicipital, scales dark reddish brown, concolorous or with very narrow pale borders; leaves ca. 20-50 cm. tall, petiole terete, short-pubescent, usually densely so, rachis terete or rarely somewhat grooved, otherwise like the petiole; lamina linear, bipinnate-pinnatifid to tripinnate-pinnatifid, pinnae deltoid, deciduously pubescent above and beneath except along the axes and midveins beneath; indusium moderately broad, deeply lobed, crispate, or as separate lobes on small ultimate segments.

The dense but very short pubescence of the petiole and rachis are especially distinctive characters. The pinnae are pinnate to bipinnate-pinnatifid; they are said to be glutinous, in drying they appear dull or shiny varnished. The related *C. micropteris* Sw. has a very narrow linear lamina, small pinnatifid pinnae about 3-6 mm. long, moderately long hairs on the rachis and narrow, tawny, concolorous rhizome scales.

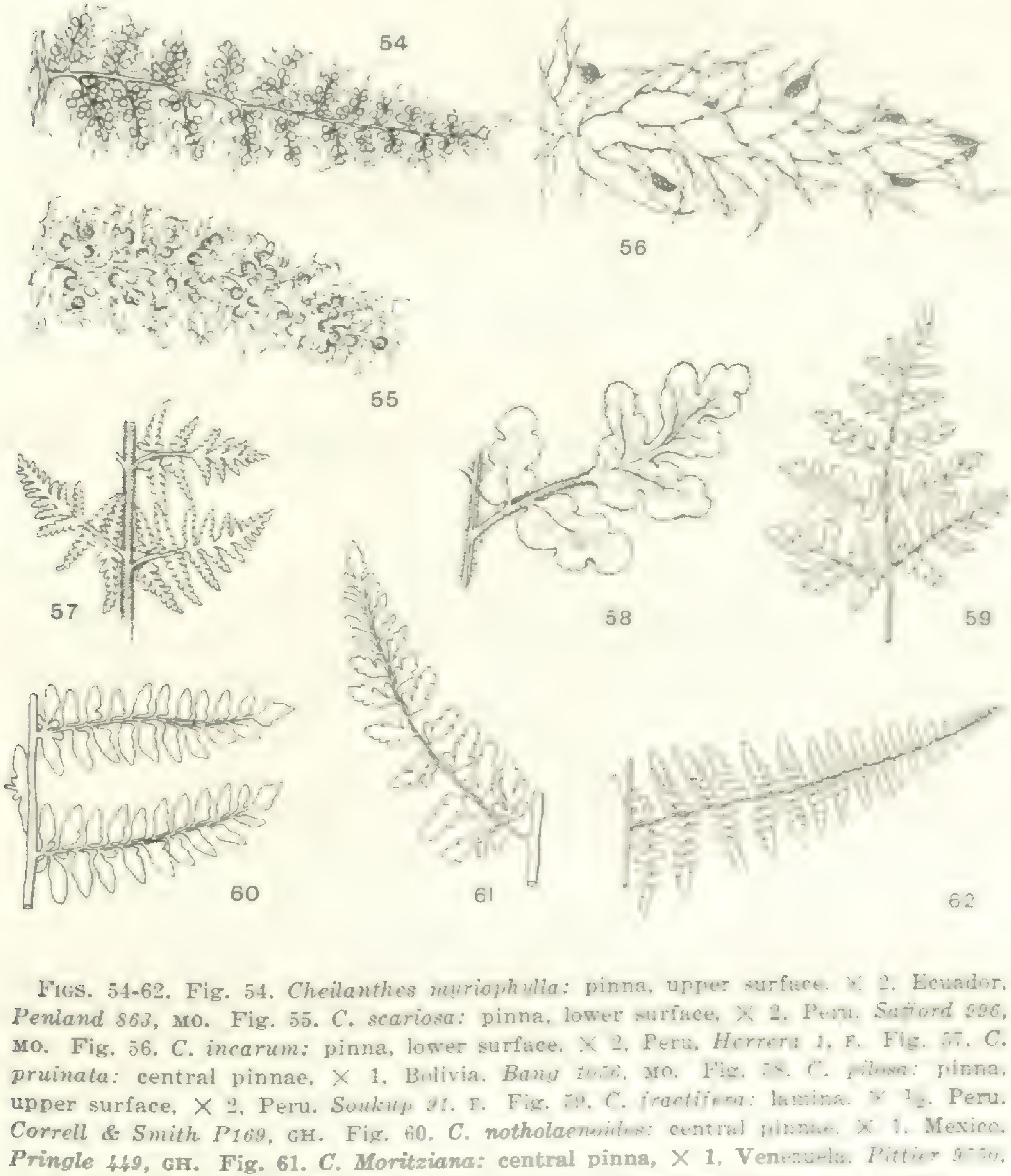
Peru to Argentina.

In crevices or on ledges of cliffs or in rocky soil, Cajamarca to Puno and Arequipa, 2800-4400 m.

Selected specimens: CAJAMARCA: Cajamarca to Cajabamba, *Ferreyra 3224* (BM, GH, USM); Cajamarca to Chilete, *Ferreyra 3324* (GH, USM). LIBERTAD: above Cachicadán, *Stork & Horton 9975* (F, UC); La Manzanas, *López 1119* (UC, US). ANCASH: Chiquián, *Ferreyra 5717* (BM), *7304* (USM), *Cerrate 500* (GH, USM), *3350* (USM). HUANUCO: Mito, *Macbride & Featherstone 1490* (F, GH, US); Panao, *Ferreyra 1943* (USM). LIMA: between Parac and Toncuyo, *Coronado 314* (GH, UC);

Matucana, *Macbride & Featherstone 420* (F, US). JUNIN: Tarma, *Killip & Smith 21807* (F, US); near Huancayo, *Killip & Smith 23362* (F, GH, US). HUANCAVELICA: se. of Pampas, *Stork & Horton 10251* (F, UC); between Conaica and Laria, *Tovar 920* (GH, USM). AYACUCHO: near Puquio, *Ferreyra 7214* (GH, USM). APURIMAC: Andahuaylas, *Stork & Horton 10717* (F and UC, in part; GH). CUZCO: Ollantaytambo, *Cook & Gilbert 360* (GH, US); near Anta, *Tryon & Tryon 5362* (BM, F, MO, U, US, USM). PUNO: Puno, *Mexia 7780* (F, GH, MO, UC, US); Araranca, *Pennell 13465* (F, GH, US). AREQUIPA: Arequipa, *Pennell 13199* (F, GH, US); 12 km. s. of Arequipa, *Eyerdam & Beetle 22126* (GH, MO, UC).

5. **Cheilanthes pilosa** Goldm. Nov. Act. Acad. Caes. Leopold.-Carol. Nat. Cur. 19, suppl. 1 (Meyen, Beitr. zur Bot.): 455. 1843. Type: Peru, *Meyen*, B! photo GH; isotype: S-PA! FIG. 58, MAP 16.



FIGS. 54-62. Fig. 54. *Cheilanthes myriophylla:* pinna, upper surface, × 2, Ecuador, *Penland 863*, MO. Fig. 55. *C. scariosa:* pinna, lower surface, × 2, Peru, *Safford 996*, MO. Fig. 56. *C. incarum:* pinna, lower surface, × 2, Peru, *Herrera 1*, F. Fig. 57. *C. pruinata:* central pinnae, × 1, Bolivia, *Bang [illegible]*, MO. Fig. 58. *C. pilosa:* pinna, upper surface, × 2, Peru, *Soukup 91*, F. Fig. 59. *C. fractifera:* lamina, × ½, Peru, *Correll & Smith P169*, GH. Fig. 60. *C. notholaenoides:* central pinnae, × 1, Mexico, *Pringle 449*, GH. Fig. 61. *C. Moritziana:* central pinna, × 1, Venezuela, *Pittier [illegible]*, GH. Fig. 62. *C. chlorophylla:* central pinna, × ½, Argentina, *Schwarz 6191*, GH.

Cheilanthes Macleanii Hook. Sp. Fil. 2: 93, t. 110B. 1852. Type: Andes of Peru, *John MacLean*, K! photo GH, US; isotype: GH!

Cheilanthes andina Hook. Sp. Fil. 2: 115. 1852. Type: Andes of Peru, *John MacLean*, K! photo GH, US.

Rhizome rather slender, short-creeping, scales lance-subulate, dark brown, rather sclerotic, with or without paler borders; leaves ca. 10-40 cm. tall, petiole terete, somewhat pubescent, the rachis similar but sometimes grooved on the upper surface; lamina lanceolate to narrowly so, bipinnate-pinnatifid to tripinnate, pinnae pubescent above and more so beneath; indusium broad, deeply crispate or lobed.

The soft spreading trichomes of the leaf and the rigid, shining rhizome scales are characteristic of this species. The rhizome is strongly multicipital although the individual branches are rather slender.

Cheilanthes andina Hook. is a variant of *C. pilosa*, perhaps a response to drier or more exposed conditions. The ultimate segments are not as broad as usual and are thicker in texture. The trichomes are frequently shorter than in the common form.

I have seen one collection that is evidently a hybrid between *C. pilosa* and *C. pruinata*: Visachani, Dept. Cuzco, *Bües 1782* (GH).

Peru to Argentina.

On ledges and in crevices of cliffs, Ancash to Puno, 2300-4200 m.

Selected specimens: ANCASH: Chiquián, *Cerrate 1548* (USM); between Llamac and Jahuacocha, *Cerrate 2337* (USM). JUNIN: near Huancayo, *Killip & Smith 23365* (US), *Saunders 647* (GH); 15 km. e. of Huancayo, *Tryon & Tryon 5467* (F). HUANCAVELICA: Cerro Santa Bárbara, near Huancavelica, *Tovar 3117* (GH, USM). CUZCO: Cerro de Cusilluyoc, *Pennell 13994* (F, GH, US); Velille, *Vargas 6541* (CUZ); Valle de Lares, *Bües 1825* (US). PUNO: Puno, *Mexia 7783* (F, GH, MO, UC, US); Araranca, *Pennell 13454* (F, GH, US); Juliaca, *Williams 2616* (US), *D. Stafford 404* (BM); Sandia, *Weberbauer 717* (B).

6. **Cheilanthes fractifera** Tryon, Rhodora 62: 7. January, 1960. Type: Dept. Ayacucho, Peru, *Correll & Smith P169*, GH! FIG. 59.

Cheilanthes Saundersii Alston, Lilloa 30: 110, t. 6. August, 1960. Type: Dept. Lima, prov. Huarochiri, Peru, *S. G. E. Saunders 350*, BM.

Rhizome short, decumbent, scales narrowly lanceolate, light brown, concolorous; leaves ca. 5-12 cm. long, petiole more or less grooved on the upper side, the ridges rounded and concolorous with the petiole, deciduous, breaking sharply and evenly toward the base, thinly whitish pubescent, as is the rachis, with large whitish scales at the base; lamina deltoid to broadly ovate, bipinnate-pinnatifid, pinnae moderately whitish pubescent with 2-5 celled trichomes beneath, thinly pubescent above; indusium more or less crenate or of small lobes, well modified.

This species was first discovered in 1954 by S. G. E. Saunders and since then it has been collected several times. The petiole that fractures evenly toward the base, the large whitish scales at the base of the petiole and the aspect of the lamina combine to make it a distinctive species among the Peruvian ones. It is closely related, however, to *C. Brandegei* of Baja California.

Peru.

Rocky hillsides, Lima to Arequipa, 1600-2200 m.

Specimens seen: LIMA: Rímac valley, dist. Surco, *Saunders 219* (BM, GH); Rímac valley, *Rauh & Hirsch P143* (B). AYACUCHO: 45 km. from Nasca on road to Puquio, *Correll & Smith P169* (GH). AREQUIPA: Cerros de Caldera, *Rauh & Hirsch P570* (B).

7. **Cheilanthes notholaenoides** (Desv.) Weath. Contrib. Gray Herb. 114: 34. 1936. FIG. 60.

Pteris notholaenoides Desv. Mém. Soc. Linn. Paris 6: 298. 1827. Type: "Hispaniola," P! photo GH.

Cheilanthes micromera Link, Hort. Berol. 2: 36. 1833. Type: "Mexico," B! photo GH.

Rhizome rather slender, creeping, more or less knotted, scales lance-subulate, brown, with or without a darker center; leaves ca. 10-20 cm. long, petiole terete, pubescent, as is the rachis; lamina narrowly lanceolate, mostly bipinnate to bipinnate-pinnatifid, pinnae slightly pubescent to nearly glabrate, except on the axes; indusium rather broad, more or less crispate, continuous.

This species is closely related to the next, *C. Moritziana*; the characters of the pinnae and rhizome scales given in the key afford a sufficient separation. In addition, the lamina of *C. notholaenoides* is rather regularly bipinnate and the pinnae are pinnate nearly to the tip, while that of *C. Moritziana* is bipinnate-pinnatifid and there is a definite pinnatifid apex of the pinnae. The rhizome is creeping but rather shortly so and it has a tendency to be multicipital.

West Indies; Mexico to Venezuela, Peru and Argentina.

Cliffs and rocky places, Piura to Junín, 2800-3300 m.

Specimens seen: PIURA: Chira valley, *Rauh P1935* (B). CAJAMARCA: 52 km. w. of Cajamarca on road to Chilete, *Correll & Smith P838* (GH). LIBERTAD: Retamas, *López & Sagástegui 3603* (GH). HUANUCO: Yanahuanca, *Macbride & Featherstone 1242* (F, GH, US). JUNIN: Ingahuasi, between Huancayo and Izcuchaca, *Tovar 3870* (GH, USM); Uspachaca, *Macbride & Featherstone 1307* (F, US).

8. **Cheilanthes Moritziana** Kze. Linnaea 23: 307. 1850. Lectotype: La Guayra (Caracas), Venezuela, *Moritz 263*, B! photo GH; isotype GH! FIG. 61.

Rhizome rather slender, creeping, sometimes knotted, scales lanceolate to lance-ovate, light brown to brown, concolorous; leaves ca. 15-40 cm. long, petiole terete, somewhat fibrillose especially on the upper side, rachis similar; lamina narrowly lanceolate, bipinnate-pinnatifid to tripinnate, pinnae only slightly pubescent above and below; indusium more or less crispate, continuous.

The differences from the closely related *C. notholaenoides* are discussed under that species. A critical study will be necessary to define *C. Moritziana* properly in relation to the Central American and Antillean *C. microphylla* Sw. It is traditionally maintained here as a segregate.

Venezuela to Colombia and Bolivia.

Sheltered, rocky places, Cajamarca and Amazonas to Cuzco, 2000-3000 m.

Specimens seen: CAJAMARCA: alrededores de San Benito, *Sagástegui 3739* (GH); Celendín, *Stübel 1045* (B); Cantanoe, Celendín to Río Marañon, *López & Sagástegui 3365* (GH); Leimabamba, valle de Utcubamba, *Stübel 1021* (B). SAN MARTIN: Salinas de Pilluana, *Ule 6900* (B). JUNIN: Muña, *Macbride 3921* (F, US). CUZCO: Yucay, *Soukup 918* (F).

9. **Cheilanthes chlorophylla** Sw. Kongl. Vet. Acad. Handl. 1817: 76. Type: Villa Rica, Brazil, *Freyreis*, (Herb. Sw.) S-PA! photo US. The material is fragmentary: a lower pinna and the central portion of a lamina. FIG. 62.

Adiantopsis chlorophylla (Sw.) Fée, Gen. Fil. 145. 1852.

Rhizome compact to creeping, scales narrowly lanceolate to subulate, bicolorous, with a dark, sclerotic central portion and lighter, thin margins; leaves ca. 15-80 cm. long, petiole shallowly grooved on the upper side, at least toward the apex, with a light colored submembranous ridge on each side, glabrate or glabrous, the rachis similar; lamina elongate-triangular, bipinnate-pinnatifid to tripinnate-pinnatifid, pinnae glabrous or glabrate; indusium suborbicular to elongate, well modified.

Ecuador s. to Bolivia and Argentina, to Brazil.

In shady woods, Cuzco, 2500-2800 m.

Specimens seen: CUZCO: Río Chaupimayo, prov. Convención, *Soukup 806* (F); Hacienda Sahuayaco, prov. Convención, *Vargas 1659* (GH); Torontoy, *Herrera 1332* (US).

10. **Cheilanthes radiata** (L.) J. Sm. Jour. Bot. Hooker 4: 159. 1841. FIG. 64.

Adiantum radiatum L. Sp. Pl. 2: 1094. 1753. LINN 1252.1, photo A, is this species.

Adiantopsis radiata (L.) Fée, Gen. Fil. 145. 1852.

? *Adiantopsis ternata* Prantl, Gartenfl. 32: 101. 1893. Type: Orinocogebiet, *Humboldt*, B! photo GH.

Rhizome erect to decumbent, often rather stout, scales subulate, bicolorous, with a dark, sclerotic central portion and lighter, thin margins; leaves ca. 10-50 cm. long, petiole glabrous, usually terete, to shallowly grooved at the apex, rachis glabrous or nearly so, grooved on the upper side with a light-colored, submembranous ridge on each side; lamina ternate, or usually radiate with up to 9 pinnae and asymmetrically circular, bipinnate, pinnae glabrous or nearly so; indusium suborbicular to oblong, well modified.

The radiate arrangement of the pinnae make this a very distinctive and attractive species. I am uncertain of the status of *Adiantopsis ternata* Prantl, FIG. 63. In addition to the type, I have seen *Pennell 3685*, *Haught 2402* and *Lehmann 2649* from Colombia and *Buchtien 7029*, *Herzog 211* and *R. S. Williams 1328* from Bolivia. This material may represent juvenile plants of *C. radiata* or, perhaps, plants growing under unusual conditions.

Tropical America.

In rocky ravines, on wooded slopes and in dense forest, Cajamarca and Amazonas to Cuzco, 200-2800 m.

Selected specimens: CAJAMARCA: Jaén, Feb. 17, 1954, *Cerrón* (GH, UC); entre Jaén y Chamaya, *López et al. 4136* (GH). AMAZONAS: Río Utcubamba, 40 km. s. of Bagua Grande, *Hutchison 1469* (GH). SAN MARTIN: Juan Jui, Alto Río Huallaga, *Klug 4170* (F, GH, MO, UC, US, USM); San José de Sisa, Prov. Lamas, *Ferreyra 7889* (GH, USM). JUNIN: La Merced, *Killip & Smith 23797* (F, US), *Macbride 5375* (F, US), *Soukup 1114, 1162* (F). CUZCO: Torontoy, *Herrera 1299* (US); Echarate; prov. Convención, *Vargas 1135* (GH).

11. **Cheilanthes farinosa** (Forsk.) Kaulf. Enum. Fil. 212. 1824. FIG. 65.

Pteris farinosa Forsk. Fl. Aegypt.-Arab. 187. 1775. Isotype: *Forskal*, BM!

Rhizome rather stout, very short-creeping, decumbent to nearly erect, scales narrowly long-triangular, brown, semi-sclerotic, concolorous; leaves ca. 10-70 cm. tall, petiole terete, to grooved on the upper side, the ridges rounded, concolorous with the petiole, slightly scaly or not, glabrous to farinaceous, rachis grooved on the upper side, glabrous to farinaceous; lamina long-triangular to ovate-triangular or narrowly so, pinnate-pinnatifid to pinnate-bipinnatifid, pinnae glabrous to somewhat ceraceous on the upper surface, conspicuously to densely white-ceraceous beneath; indusium crispate, lobed, more or less continuous, well modified.

This is a most distinctive species because of the white waxy covering of the segments which is especially evident on their under surface.

West Indies; Mexico to Peru; Old World.

Rocky places, Huánuco to Cuzco, ca. 2000 m.

Specimens seen: HUANUCO: Muña, *Bryan 555* (F, US). JUNIN: near Huacapistana, *Tryon & Tryon 5435* (F). CUZCO: Nevada Sallcantay, *Bües 986* (US).

12. **Cheilanthes Poeppigiana** Kuhn, Linnaea 36: 84. 1869. Type: Peru, *Poeppig*. FIG. 66, MAP 17.

Rhizome small, short, scales subulate-lanceolate with a dark brown sclerotic central portion and paler, thinner borders; leaves ca. 8-35 cm. tall, petiole grooved on the upper side, the ridges rounded, concolorous with the petiole, slightly scaly to glabrate, rachis similar, but with narrow green wings on the upper side, at least toward the apex; lamina oblong-lanceolate to deltoid, pinnate-pinnatifid to bipinnate-pinnatifid, pinnae glabrous, pinnules adnate to somewhat narrowed at the base; indusium continuous, intramarginal, well modified.

Small laminae of this species may be lanceolate; large ones are ovate or broadly triangular. The segments are relatively broad and herbaceous and their broadly attached base is characteristic.

Ecuador to Argentina.

Crevices of cliffs or Inca walls, among rocks in ravines and on shrubby slopes, Tumbes to Puno, 150- (usually 1700-2200) 3000 m.

Selected specimens: TUMBES: between Tumbes and Cancho, *Coronado 226* (GH, UC). LAMBAYEQUE: entre Beatita de Humay y km. 38 (Carretera Olmos-Marañon), *López et al. 4042* (GH); 27 km. e. of Olmos on road to Jaén, *Correll & Smith P802* (GH). CAJAMARCA: entre Cascas y Contumazá, *López et al. 3725* (GH). LIBERTAD: Huaranchal, *Sagástegui 194* (GH). HUANUCO: Piedra Grande, *Macbride 3672* (F). JUNIN: Huacapistana, *Tryon & Tryon 5436* (BM, F, MO, U, US, USM); Carpa-

FIGS. 63-69. Fig. 63. *Cheilanthes ternata:* lamina, × ½, Colombia, *Pennell 3685*, GH. Fig. 64. *C. radiata:* lamina, × ¼, Venezuela, *Fendler 67*, GH. Fig. 65. *C. farinosa:* lamina, × ½, Mexico, *Pringle 10816*, GH. Fig. 66. *C. Poeppigiana:* central pinnae, × ¾, Bolivia, *Fiebrig 3164*, GH. Fig. 67. *C. Orbignyana:* A, fertile pinna, × ½, Peru, *Sagástegui 2937*, GH; B, sterile pinna, × 1, *idem*. Fig. 68. *C. rufopunctata:* base of fertile pinna, × 4, Peru, *Vargas 5007*, MO. Fig. 69. *C. marginata:* base of fertile pinna, × 4, Peru, *Macbride 3326*, F.

pata, *Cerrate 2808* (GH). CUZCO: Machu-Picchu, *Tryon & Tryon 5396* (BM, F, MO, U, US, USM), *Mexia 8085* (F, GH, MO, US). PUNO: Sandia, *Weberbauer 566* (B).

13. **Cheilanthes Orbignyana** Kuhn, Linnaea 36: 82. 1869. Type: Prov. La Laguna, Bolivia, *D'Orbigny 388;* isotype: P, photo GH. FIG. 67.

Rhizome erect, moderately stout, scales lanceolate or narrowly so, brown to dark brown, concolorous, semi-sclerotic; leaves ca. 25-50 cm. long, petiole shallowly grooved on the upper side, at least toward the apex, flat to convex between the small, rounded ridges which are concolorous with the petiole, glabrous or nearly so, rachis similar but the ridges somewhat lighter in color and rather sharp; lamina narrowly ovate, tripinnate-pinnatifid to quadripinnate, pinnae glabrous to slightly glandular; indusium suborbicular to lunate, well modified.

Peru and Bolivia.
Among rocks, Cajamarca, 2750 m.

Specimen seen: CAJAMARCA: La Pampa, Guzmango, *Sagástegui 2937* (GH).

MAPS 17-18. Map 17, *Cheilanthes Poeppigiana.* Map 18, *C. marginata.*

14. **Cheilanthes rufopunctata** Rosenst. Meded. Rijks Herb. Leiden 19: 9. 1913. Type: Araca, Bolivia, *Herzog 2366;* fragment US!; L, photo GH. FIG. 68.

Rhizome creeping, often knotted, scales lanceolate long-triangular, reddish brown, wholly sclerotic; leaves ca. 15-35 cm. tall, petiole grooved on the upper side, at least toward the apex, deeply sulcate between the relatively large, rounded ridges which are concolorous with the petiole, glabrous, rachis grooved and glabrous, with green wings toward the apex; lamina long-deltoid to broadly lanceolate, tripinnate to tripinnate-pinnatifid, pinnae glabrate above and beneath, or with numerous reddish, sessile glands, especially beneath, indusium broad, crispate, well modified.

Cheilanthes glauca (Cav.) Mett. of Chile, which is related to this species, has a pentagonal lamina, the segments of which are thickly beset beneath with short, dark trichomes which also extend in lines along the sides of the pinna-rachises and the rachis.

Peru and Bolivia.

Rock crevices, Lima to Puno, 2600-4000 m.

Selected specimens: LIMA: Matucana, *Macbride & Featherstone 285* (F, GH, US), *Rauh P181* (B); Viso, *Macbride & Featherstone 759* (photos F, US). JUNIN: Huancayo, *G. Kunkel 482* (GH). HUANCAVELICA: near Conaica, *Tovar 316* (GH, US, USM). CUZCO: Valle de Lares, *Soukup 29* (F, US); Calca, *Vargas 4004* (CUZ, UC, US); Canchis, *Vargas 5007* (MO, US). PUNO: near Puno, *Vargas 29* (MO), *Soukup 29* (UC); Vilcanota, *Rauh P706* (B).

15. **Cheilanthes marginata** HBK. Nov. Gen. Sp. 1: 22. 1815. Type: Penipe, Quito, Ecuador, *Humboldt & Bonpland*, P! photo GH. FIG. 69, MAP 18.

Rhizome short-creeping, somewhat multicipital, scales ovate-lanceolate, attenuate, dark brown, sclerotic; leaves ca. 8-25 cm. tall, the petiole sulcate, the ridges rounded, concolorous with the petiole, somewhat scaly, rachis sulcate, with green wings on the upper side above the base; lamina broadly deltoid to lanceolate, mostly tripinnate, pinnae glabrous, ultimate segments stalked or narrowed at the base; indusium glandular-fimbriate, continuous along the margins and decurrent on the axes of the pinnules and pinnae.

The unusual condition of the indusium which extends from the segments along their stalks and along the pinna-rachises mark this species as one of the most distinctive in Peru.

Venezuela to Colombia, south to Argentina.

Cliffs, among rocks and in rocky soil, Piura to Puno, 2200-4000 m.

Selected specimens: PIURA: near Ayabaca, 1927, *Berry* (US). LIBERTAD: Huaranchal, *Sagástegui 207, 2664* (GH). CAJAMARCA: Cajamarca to Chilete, *Ferreyra 3294* (USM); El Puquio, Guzmango, *Sagástegui 3918* (GH). ANCASH: e. of Huasta, *Cerrate 2264* (USM). HUANUCO: Mito, *Macbride 3326* (F, GH, US), *Bryan 195* (F). PASCO: between Salcachupán and Cerro de Pasco, *Ferreyra 6619* (GH, USM). JUNIN: Huancayo, *G. Kunkel 481* (GH). HUANCAVELICA: Colcabamba to Paurcarbamba, *Tovar 1969* (USM). AYACUCHO: Pampalca, *Killip & Smith 22234* (US). CUZCO: Machu-Picchu, *Tryon & Tryon 5401* (BM, F, MO, U, US, USM), *Ferreyra 2684* (GH); Valle de Lares, *Bües 1798* (US). PUNO: Sandia, *Soukup 157* (F), *Weberbauer 718* (B).

FIG. 70. *Notholaena nivea*, Cuzco area.

16. NOTHOLAENA R. Br. Prod. Fl. Nov. Holl. 145. 1810: Type: *Acrostichum Marantae* L. = *Notholaena Marantae* (L.) Desv. FIG. 70.

Terrestrial, the rhizome small to moderately stout, compact to creeping, scaly, bearing the leaves in a cluster or loosely spaced; leaves small to medium sized, pinnate-pinnatifid to quadripinnate, glabrous, ceraceous, pubescent or scaly, veins free; sporangia borne on the apical ½ to ¼ of the vein or at its tip, partially covered by an indusium formed from the reflexed, slightly modified margin, or the margin reflexed to plane and unmodified, paraphyses absent. — 62 American species.

Tryon, R. A revision of the American species of Notholaena. Contrib. Gray Herb. 179. 1956.

Weatherby, C. A. The Argentine species of Notholaena. Lilloa 6: 251-275. 1941.

These are small ferns with tufts of leaves, characteristic of the xeric and semi-xeric rocky places of the Altiplano and the higher elevations of the eastern and western Andean valleys. The leaves resist desiccation to a considerable degree and the roots evidently draw on local sources of water (perhaps night condensation in part) for the plants are usually fresh when other vegetation is dry and dormant. The rhizome contains a persistent (up to 50 years in herbarium specimens) oily substance which may well be related to its water-holding capacity.

Notholaena tomentosa Desv., with pubescent leaves and a strongly sulcate petiole and rachis, is reported from Peru by Pichi-Sermolli (Webbia 8: 181, 186, 1951) but the records must be considered as dubious until they have been confirmed by modern collections.

KEY TO SPECIES

a. Indument of the lamina of scales or trichomes, or both, not ceraceous. .... b.

  b. Indument of the lamina of scales (in *N. sinuata* some of these may be dissected into capillary lobes), sometimes also of trichomes. .... c.

    c. Indument of scales only. .... d.

      d. Lamina lanceolate or broader, bipinnate to tripinnate, pinnae few; petiole commonly at least half as long as the lamina, with one vascular bundle. .... e.

e. Scales of the rhizome entire or minutely serrulate with very short ascending teeth; scales of the upper surface of the lamina soon deciduous, lance-subulate, flat, or if narrow and subpiliform then 1 mm. or less long, scales of the lower surface erose-serrulate with mostly deltoid teeth. .... f.

f. Lamina lanceolate, mostly 12-18 cm. tall; rhizome scales entire or nearly so; scales of the blade dark chestnut brown; dilated soriferous vein ends projecting into small, hyaline, marginal lobes. .... 1. *N. peruviana*

f. Lamina deltoid-ovate, mostly 2-4.5 cm. tall; rhizome scales minutely serrulate; scales of the lower surface of the lamina bright or pale brown; soriferous vein-ends in slight, unmodified crenations of the margin. .... 2. *N. arequipensis*

e. Scales of the rhizome remotely antrorse-serrulate; scales of the upper surface of the lamina piliform, more or less persistent, more than 1 mm. long, scales of the lower surface pectinate-serrulate, with often piliform, although broad-based, teeth. .... g.

g. Lamina ovate or elliptic, about equaling, or shorter than the petiole; piliform scales of the upper surface of the lamina brown, those of the lower surface lance-ovate or ovate, 3-4 mm. long. .... 3. *N. squamosa*

g. Lamina lanceolate, much longer than the petiole; piliform scales of the upper surface of the lamina whitish, those of the lower surface lance- or linear-subulate, up to 2 mm. long. .... 4. *N. lonchophylla*

d. Lamina linear with numerous merely lobed pinnae; petiole much shorter than the lamina, with two vascular bundles. .... 5. *N. sinuata*

c. Indument of both scales and trichomes. .... 6. *N. cantangensis*

b. Indument of the lamina of trichomes only. .... h.

h. Indument of simple trichomes. .... i.

i. Lamina bipinnate, much longer than the petiole, segments appressed and ascending pubescent beneath. ...... 7. *N. obducta*

i. Lamina not much longer than the petiole, or if so, then uniformly pinnate-pinnatifid. .... j.

j. Lamina gradually reduced at base, usually much longer than the petiole, uniformly pinnate-pinnatifid, the pinnae equilateral, long-deltoid to oblong; rhizome short, ascending, knotted, the tips of the scales dark brown. .... 8. *N. aurea*

j. Lamina not conspicuously reduced at the base, nor much longer than the petiole, pinnate-pinnatifid, the pinnae inequilateral, deltoid; rhizome creeping, horizontal, the tips of the scales light brown. .... 9. *N. Fraseri*

h. Indument of stellate trichomes. .... 10. *N. mollis*

a. Indument of lamina wholly ceraceous, or lacking. .... k.

k. Rhizome scales bicolorous, with a dark brown to blackish central portion and narrow, lighter margins; pinnules adnate or predominantly so. .... 11. *N. sulphurea*

k. Rhizome scales concolorous, brown; pinnules stalked, or some of them sessile. .... l.
  l. Ultimate segments persistent, mostly orbicular or nearly so; rhizome scales oily. .... 12. *N. Stuebeliana*
  l. Ultimate segments articulate, oblong to ovate, or some of them nearly orbicular; rhizome scales dry. .... 13. *N. nivea*

1. **Notholaena peruviana** Desv. Mém. Soc. Linn. Paris 6: 220. 1827. Type: Peru, *Dombey*, P! photo GH, UC, fragment B! FIG. 71.

Notholaena Brackenridgei Baker, Syn. Fil. 371. 1868. Type: Peru, *Brackenridge* (evidently Baños, Peru, Wilkes Exped.), K! photo GH; isotype: US!

Rhizome erect, stout, scales linear-ligulate, long-attenuate, margins entire or nearly so; leaves to 30 cm. tall, the petiole somewhat shorter to much shorter than the lamina, with one vascular bundle; lamina narrowly lanceolate, not narrowed below, bipinnate to tripinnate, with some pinnules lobed, the lower surface densely covered with dark brown, lanceolate to ovate, somewhat pectinate-serrulate scales; sporangia borne on the vein-ends, the margin modified, narrow.

This and the next species are closely related and may be separated by the characters mentioned in the key. From *N. lonchophylla*, they are distinguished by the deciduous rather than persistent scales on the upper surface of the lamina, of different shape, and the erose-serrulate, rather than pectinate-serrulate scales, on the lower surface. The lamina of *N. lonchophylla* is proportionately narrower than in *N. peruviana* or *N. arequipensis* and the pinnae are more regularly divided.

Peru.

In soil and on rocks of lomas, and on exposed rocky slopes, Lambayeque to Moquegua, 300-3900 m.

Selected specimens: LAMBAYEQUE: 44 km. from Olmos on road to Jaén, *Correll & Smith P822* (GH). CAJAMARCA: entre Cascas y Contumazá, *López et al. 3688* (GH); El Puquio, Guzmango, *Sagástegui 3917* (GH). LIBERTAD: Huaranchal, prov. Otuzco, *López et al. 2442* (GH). LIMA: High Mts. above Lima, *Stafford 999* (F, US), *1000* (US); Matucana, *Macbride & Featherstone 284, 121* (F), *Bryan 43* (F); above San Bartolomé, *Ferreyra 9742* (GH, USM); above Surco, *Ferreyra 3458* (GH,USM). AREQUIPA: Mollendo, *Dora Stafford 824* (BM); Mollendo (loma), *Weberbauer 1528* (B); Lomas de Capac, near Chala, *Ferreyra 1426* (USM), *Coronado 39* (GH, UC, US); Lomas de Atiquipa, *Coronado 35* (GH, UC, US); Lomas de Chaparra, cerca Chala, *Ferreyra 11968* (GH, USM). MOQUEGUA: Ilo, *Dora Stafford 933* (BM).

2. **Notholaena arequipensis** Maxon, Smiths. Misc. Coll. 65(8):9. 1915. Type: near Arequipa, Peru, *Rose & Rose 18797*, US! photo GH. FIG. 72.

Rhizome erect or ascending, scales linear, long-attenuate, distantly denticulate with ascending teeth; leaves to 8 cm. tall, petiole somewhat longer than the lamina, with one vascular bundle; lamina deltoid-oblong, bipinnate, the pinnules hardly if at all lobed, the lower surface densely covered with large, ovate-oblong, long-acuminate, light reddish brown, erose-denticulate scales; sporangia borne on the vein-ends, the margin somewhat revolute, unmodified.

A local species and one closely related to the previous; the characters by which the two may be distinguished are presented in the key.

Southern Peru to n. Chile and nw. Argentina.

Rocky places and crevices of rocks, Arequipa, 2200-2750 m.

Specimens examined: AREQUIPA: Arequipa, *Rose & Rose 18797* (US), *R. S. Williams 2638* (GH, NY, US), *Pennell 13116* (F), *13198* (B, F, GH), *Jaffuel 2561* (GH); Yura, *Vargas 8019* (UC); Quebrada de San Lazaro, *Munz 15500* (GH); El Misti, *D. Stafford 570* (BM), *Cárdenas & Rodriguez 20* (F).

3. **Notholaena squamosa** (Hook. & Grev.) Lowe, Ferns Brit. & Exot. 1: 49. 1856. FIG. 73.

Cheilanthes squamosa Hook. & Grev. Icon. Fil. t. 151. 1829. Type: Cerro del Morro, San Luis, Argentina, *Gillies*, E; isotype: K!

Pellaea Lilloi Hicken, Anal. Soc. Cient. Argent. 62: 210. 1906. Type: Tucumán, Argentina, *Lillo 5021*, SI! photo GH.

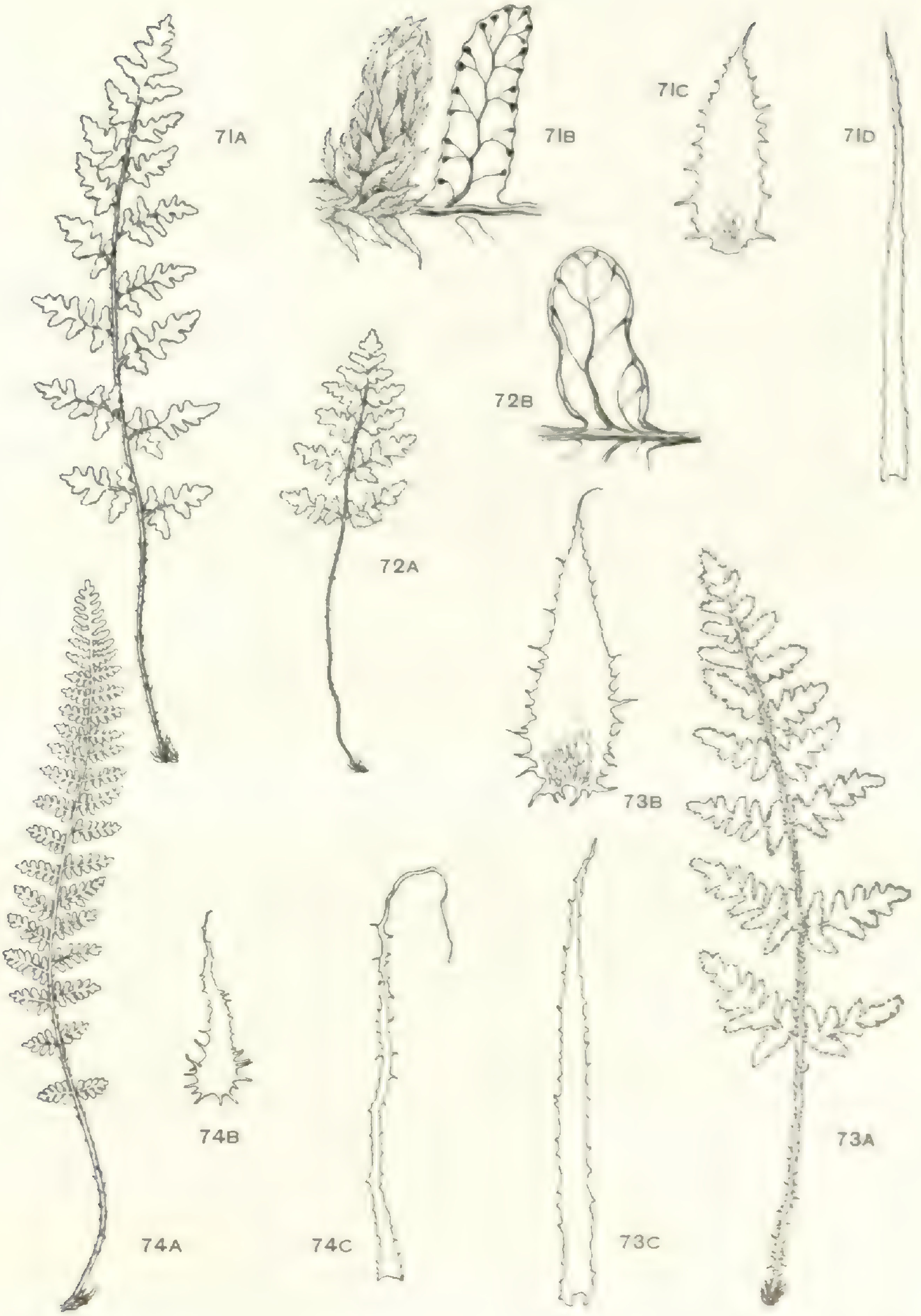
Notholaena Lilloi (Hicken) Hicken, Apuntes Hist. Nat. Buenos Aires 1: 117. 1909.

Rhizome short, erect or oblique, scales thick, subsclerotic, linear, tapering to a long capillary point, pectinate-serrulate, the teeth often antrorse; leaves to 30 cm. tall, petiole about half as long as, to somewhat longer than, the lamina, with one vascular bundle; lamina oblong-lanceolate to broadly ovate, bipinnate, the lower surface densely covered with soft, imbricate, brown, lance-ovate to ovate, pectinate-fimbriate scales; sporangia at the apex of the veins, margin unmodified.

Southern Peru to Argentina.

Calcareous hills, Puno, 3900 m.

Specimen seen: PUNO: Camjata Hacienda, Capachica peninsula (Lake Titicaca), *Tutin 1032* (BM).



FIGS. 71-74. Fig. 71. *Notholaena peruviana:* A, leaf, × ½, Peru, *J. B. Steere*, MO; B, segments, lower surface, × 4½, *idem;* C, scale from lower surface of segment, × 9, *idem;* D, rhizome scale, × 4½, *idem.* Fig. 72. *N. arequipensis:* A, leaf, × ½, Peru, *Pennell 13116*, F; B, segment, × 4½, *idem.* Fig. 73. *N. squamosa:* A, leaf, × ½, Argentina, *Castillón 11615*, GH; B, scale from lower surface of segment, × 9, *idem;* C, rhizome scale, × 4½, *idem.* Fig. 74. *N. lonchophylla:* A, leaf, × ½, Peru, *Mathews 610*, K; B, scale from lower surface of segment, × 9, *idem;* C, rhizome scale, × 4½, *idem.*

4. **Notholaena lonchophylla** Tryon, Contrib. Gray Herb. 179: 19. 1956. Type: Peru, *Mathews 610*, K! photo GH. FIG. 74.

Rhizome short, horizontal or ascending, scales linear-ligulate, sparingly antrorsely denticulate; leaves to 15 cm. tall, petiole shorter than the lamina, with one vascular bundle; lamina lanceolate, pinnate-pinnatifid to bipinnate, the lower surface densely covered with pale brown to whitish, linear-subulate, long-acuminate, pectinate-dentate scales; sporangia at the apex of the veins, margin unmodified.

Although one of the most recently described species from Peru this is also the rarest; quite possibly it is extinct. The single plant collected by Mathews in 1835 is our sole record. For the benefit of anyone keen enough and fortunate enough to find it, the differences from the related *N. peruviana* and *N. arequipensis* are discussed under the former species.

Endemic to Peru.

Specimen examined: PERU: 1835, *Mathews 610* (K).

5. **Notholaena sinuata** (Sw.) Kaulf. Enum. Fil. 135. 1824, var. **sinuata.** FIG. 75, MAP 19.

Acrostichum sinuatum Sw. Syn. Fil. 14. 1806. Type: Peru, "*Squamaria sinuata*, Lagasca Herb." (Herb. Sw.), S-PA!

Notholaena Tectaria Desv. Mém. Soc. Linn. Paris 6: 219. 1827. Type: Peru, P! photo GH. Tarma, *Dombey*, "*N. Tectaria* Desv. ex Desv." B! is probably an isotype, as is Tarma, *Dombey*, BM!

Rhizome short, horizontal, scales linear to linear-subulate, pectinate-ciliate to entire; leaves up to 45 cm. tall, petiole usually less than ¼ the length of the lamina, with two vascular bundles; lamina linear, pinnate-pinnatifid, the lower surface thickly covered with castaneous or pale brown, deltoid to lanceolate, acuminate, short-fimbriate scales, these overlying a tomentum of smaller scales dissected into long capillary segments; sporangia borne on the terminal portion of the veins, margin unmodified.

The two vascular bundles in the petiole serve to distinguish this species from the others of the genus. In addition, the scaly, linear lamina, much longer than the petiole, and the lobed pinnae are characteristic. Many of the scales on the segments are dissected into capillary processes, giving the indument as a whole a tomentose appearance.

The species is distributed from Argentina to Colombia and Venezuela, and northward to the southwestern United

States and in Hispaniola. In Mexico and the southwestern United States there also occur two other varieties.

Crevices of rocks, rocky banks and hillsides, Lambayeque, Cajamarca and Amazonas to Cuzco and Arequipa, 1000-3800 m.

Selected specimens: LAMBAYEQUE: 20 km. from Olmos on road to Jaén, *Correll & Smith P795* (GH). CAJAMARCA: entre Cascas y Contumazá, prov. Contumazá, *López et al. 3687* (GH). AMAZONAS: Tambo de Carrizal, *Stübel 1041*, in part (B). LIBERTAD: Huaranchal, *Sagástegui 210* (GH). ANCASH: s. of Chiquián, *Cerrate 7589* (USM). HUANUCO: Ambo, *Macbride 3190* (F, US); Mito, *Macbride & Featherstone 2310* (F, GH, US). LIMA: Santa Eulalia, *Goodspeed 11307* (GH, MO, UC); between Surco and Matucana, *Ferreyra 5434* (USM). JUNIN: Tarma, *Killip & Smith 21808* (US); Cerro San Sebastián, Tarma, *Ferreyra 530* (GH, USM). AYACUCHO: Nasca to Puquio, *Correll & Smith P171B* (LL). CUZCO: Quillabamba, *Stork et al. 10449* (MO). AREQUIPA: near Arequipa, *D. Stafford 1289* (BM); Tiabaya, *Pennell 13071* (F, GH); Yura, prov. Arequipa, *Vargas 8018* (UC).

6. **Notholaena cantangensis** Tryon, Rhodora 63: 81. 1961. Type: Cantange, prov. Celendín, Dept. Cajamarca, Peru, *López & Sagástegui 3366*, GH! FIG. 76.

Rhizome short, scales lanceolate with a dark, sclerotic central portion and brown, pectinate-serrulate margins; leaves 10-15 cm. tall, petiole shorter than the lamina, with one vascular bundle; lamina lanceolate-elliptic, bipinnate-pinnatifid, the lower surface covered with narrowly ovate-lanceolate scales, the upper surface moderately pubescent with rather short and thick trichomes; sporangia borne at the apex of the veins, margin slightly modified.

Peru.

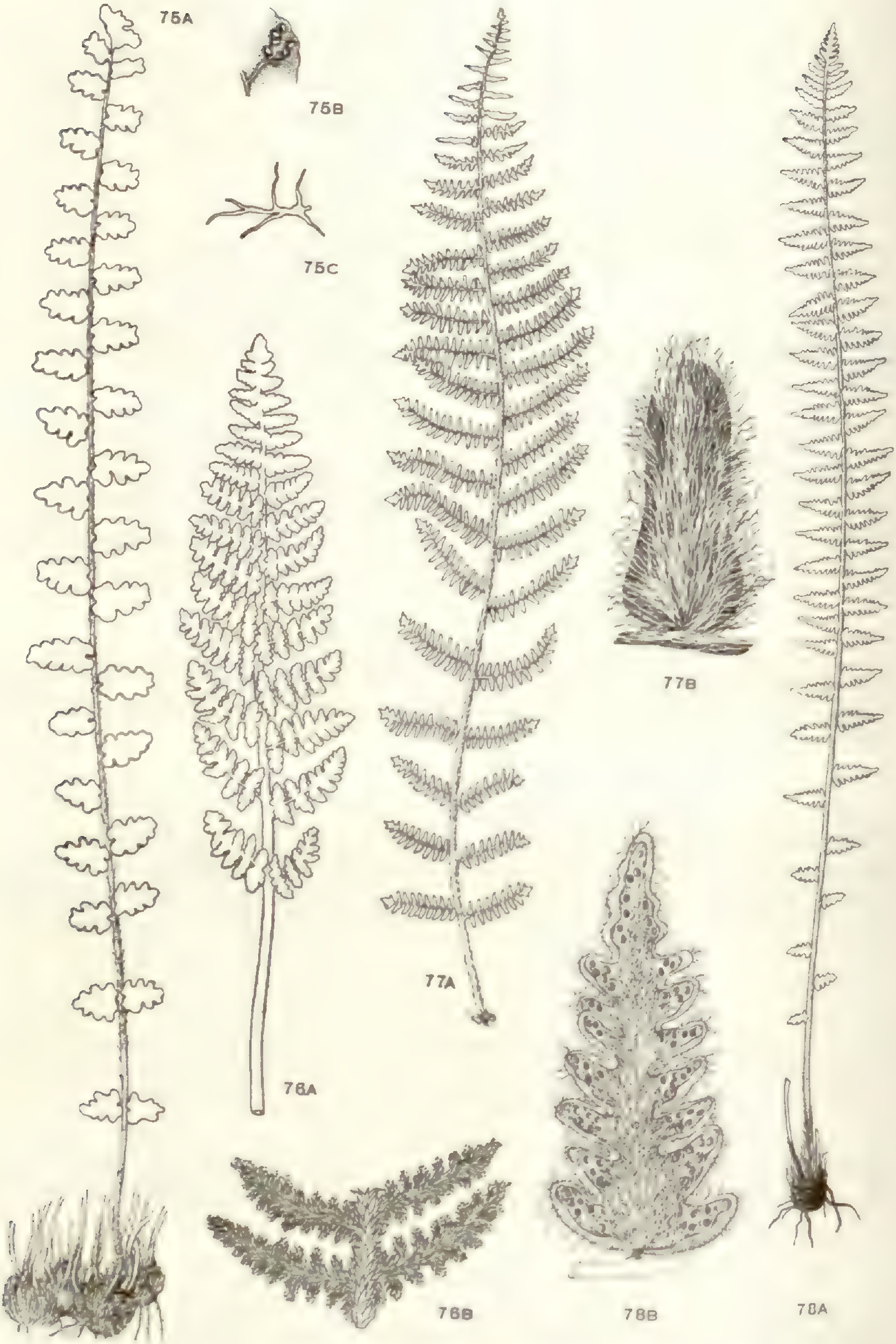
Among rocks, Cajamarca, 1450 m.

Specimen seen: CAJAMARCA: Cantange, ruta Celendín-Río Marañon, *López & Sagástegui 3366* (GH).

7. **Notholaena obducta** (Kuhn) Baker, Syn. Fil. ed. 2, 515. 1874. FIG. 77.

Cheilanthes obducta Kuhn, Linnaea 36: 83. 1869. Type: Bolivia, *D'Orbigny 386*, B! photo GH.

Rhizome short-repent, scales narrowly linear, pale brown, or with a castaneous, sclerotic central portion and lighter margins; leaves to 55 cm. long, petiole much shorter than the lamina, with one vascular bundle; lamina lanceolate, bipinnate, the lower surface densely sub-



FIGS. 75-78. Fig. 75. *Notholaena sinuata* var. *sinuata:* A, leaf, × ½, New Mexico, U. S., *Wooton* in 1895, MO; B, sori, enlarged, *idem;* C, scale from upper surface of lamina, enlarged, *idem.* Fig. 76. *N. cantangensis:* A, lamina, × ¾, Peru, *López & Sagástegui 3366*, GH; B, central pinnae, lower surface, × 1, *idem.* Fig. 77. *N. obducta:* A, leaf, × ½, Paraguay, *Rojas 13656*, MO; B, segment, lower surface, × 7, *idem.* Fig. 78. *N. aurea:* A, leaf, × ½, Texas, U. S., *E. J. Palmer 30608*, MO; B, pinna, lower surface, × 4½, *idem.*

appressed pubescent, the trichomes rather straight, sporangia borne at the apex of the veins, margin unmodified.

The trichomes on the lower surface of the pinnae are unusual, having from 3 to 6 of the lower cells branching from the trichome proper.

Colombia, Peru, Bolivia to Paraguay.

Under shrubs and trees, Cajamarca, 680 m.

Specimen seen: CAJAMARCA: Valley of the Río Chamaya, Mesones to Muro, highway between Olmos and Río Marañon, *Hutchison 1425* (UC).

8. **Notholaena aurea** (Poir.) Desv. Mém. Soc. Linn. Paris 6: 219. 1827. FIG. 78, MAP 20.

Pteris aurea Poir. Lam. Encycl. Méth. 5: 710. 1804. Type: Peru, *Joseph de Jussieu* (Herb. Jussieu no. 1033), P! photo GH.

Notholaena ferruginea (Link) Hook. Second Cent. Ferns, sub t. 52. 1861.

Notholaena bonariensis (Willd.) C. Chr. Ind. Fil. 6. 1905; 459. 1906.

MAPS 19-20. Map 19, *Notholaena sinuata* var. *sinuata*. Map 20, *N. aurea*.

Rhizome short-repent, knotted, scales lance-linear, entire; leaves to 60 cm. tall, petiole 1/3 as long as the lamina or less, with one vascular bundle; lamina linear-elliptic, long-attenuate at the base, pinnate-pinnatifid, the lower surface covered with a dense tawny (white when young) tomentum of fine matted trichomes; sporangia borne on the vein-ends, margin modified with a very narrow subhyaline band.

Notholaena aurea is one of the characteristic ferns of the Altiplano. It is usually quite distinctive in the aspect of its pubescent lamina but some variations must carefully be distinguished from *N. Fraseri.*

Southwestern United States to Chile and Argentina; West Indies.

On soil banks, rocky slopes, shrubby hillsides or cliffs, Lambayeque and Amazonas to Arequipa and Puno, 1200-3200 m.

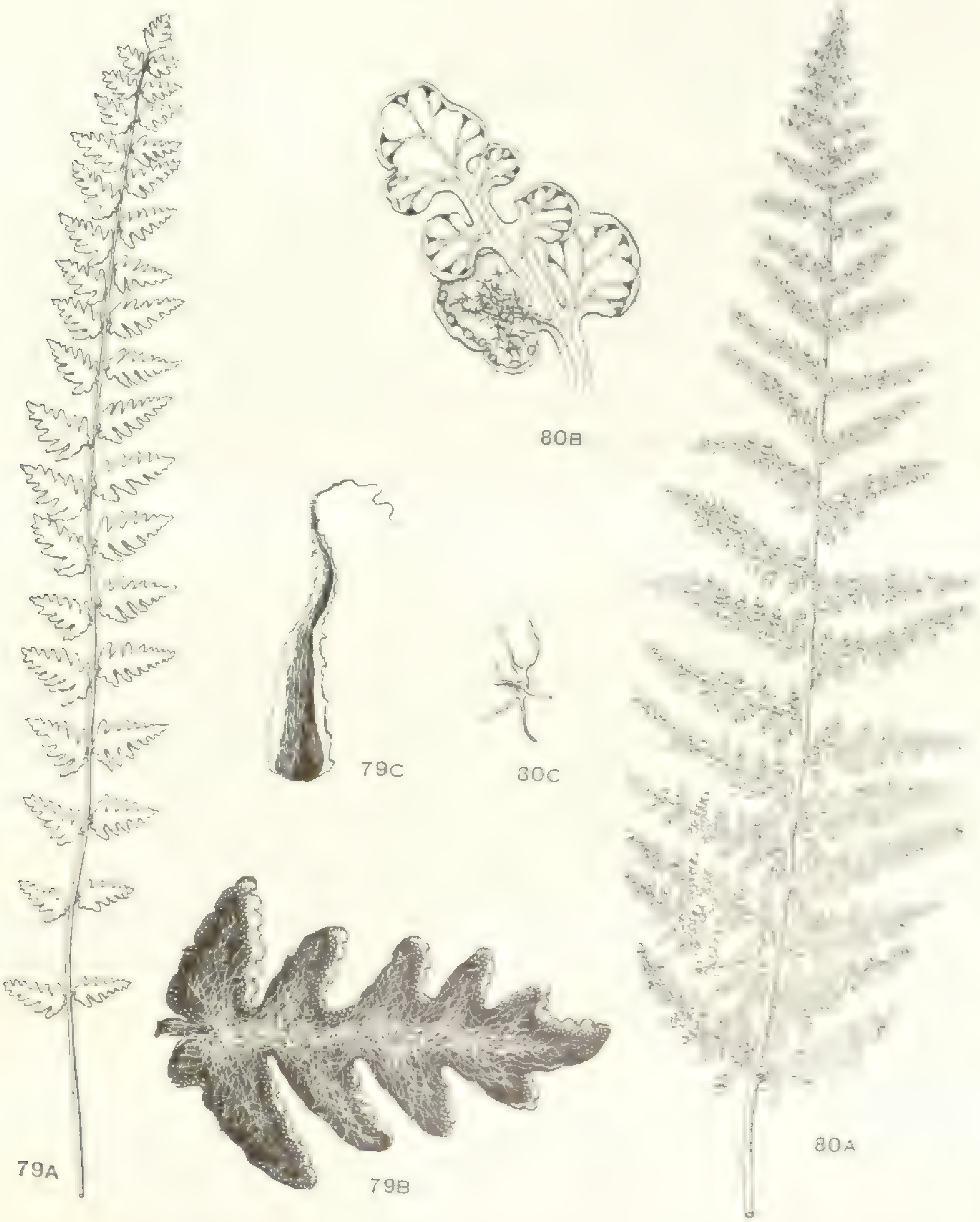
Selected specimens: LAMBAYEQUE: 44 km. from Olmos on road to Jaén, *Correll & Smith P821* (GH). AMAZONAS: Prov. Chachapoyas, *Matthews 205* (BM, K), *3289* (B); Tambo de Carrizal, *Stübel 1041*, in part (B). LIBERTAD: Huaranchal, *Sagástegui 211* (GH); Munmalca, prov. Huamachuco, *López & Sagástegui 2826* (GH). ANCASH: Chiquián, *Ferreyra 5786* (USM), *Cerrate 788* (USM). HUANUCO: Mito, *Macbride & Featherstone 1921* (F, US); between Ambo and Huanuco, *Ferreyra 9234, 10394* (GH, USM). LIMA: Oroya RR., *Safford 991* (F, GH, P, US); Cajatambo, *Ferreyra 3545* (USM); Matucana, *Macbride & Featherstone 370, 423* (F). JUNIN: Carpapata to Huacapistana, *Ferreyra 11020* (GH, USM); Vilcabamba, *Tryon & Tryon 5421* (F, BM, MO, U). HUANCAVELICA: between Salcabamba and Surcubamba, *Tovar 1812* (GH, USM); 4 km. s. of Conaica, *Tovar 970* (GH, USM). AYACUCHO: Pampalca, *Killip & Smith 22256* (F, US). APURIMAC: Andahuaylas, *Stork & Horton 10717* (F, UC). CUZCO: Ollantaytambo, *Cook & Gilbert 361* (US), *695* (US); Calca, *Vargas 3136* (F). PUNO: Sandia, *Weberbauer 721* (B). AREQUIPA: Arequipa, *D. Stafford 589* (BM); near Laspinas, prov. Arequipa, *Eyerdam & Beetle 22144* (GH).

9. **Notholaena Fraseri** (Kuhn) Baker, Syn. Fil. ed. 2, 83. 1874. FIG. 79, MAP 21.

Cheilanthes Fraseri Kuhn, Linnaea 36: 83. 1869. Syntypes: Ecuador, *Fraser Wagner* and Peru, *Ruiz & Pavon*, B! (a sheet containing both collections) photo GH.

Rhizome short- to moderately long-repent, scales narrowly linear-subulate, entire or remotely serrulate; leaves to 40 cm. tall, petiole about half as long as the lamina, with one vascular bundle; lamina narrowly linear, pinnate-pinnatifid or bipinnatifid at the base, the lower surface densely tomentose with rather coarse, matted pale brown trichomes; sporangia borne on the vein-tips, margin slightly modified.

The differences between this species and the sometimes similar *N. aurea* are presented in the key. *Notholaena Buchtienii* Rosenst., a species of Bolivia, may well also occur in Peru. It is quite closely related to *N. Fraseri* and the two may be separated as follows:



FIGS. 79-80. Fig. 79. *Notholaena Fraseri:* A, leaf, × ½, Peru, *Stork et al.* [illegible], F; B, pinna, upper surface, × 4½, Peru, *Mexia* [illegible], MO; C, rhizome scale, × 18, *idem.* Fig. 80. *N. mollis:* A, leaf, × ½, Chile, *Wagenknecht* 18571, MO; B, pinnule, × 4½, *idem;* C, trichome from lamina, enlarged, *idem.*

Rhizome with numerous pale scales with conspicuously tortuous capillary tips, giving a tomentose appearance; no scales on rachis or upper part of petiole; median pinnae mostly deltoid, veins not visible on the upper surface. .... *N. Fraseri*

Rhizome usually with a few and inconspicuous pale, capillary-tipped scales, not appearing tomentose; a few deciduous scales among the tomentum on the upper part of the petiole and the lower part of the rachis; median pinnae mostly lanceolate or deltoid-lanceolate, the veins usually subimpressed and visible on the upper surface. .... *N. Buchtienii*

Ecuador to Bolivia.

Rocky places, often shaded, Piura to Cuzco, 1000-3500 m.

Selected specimens: PIURA: Huancabamba, *Scolnik 1435* (UC). CAJAMARCA: Santa Cruz, *Weberbauer 4139* (B); between San Marcos and Cajabamba, *Correll & Smith P909* (GH). HUANUCO: Huánuco, *Macbride & Featherstone 2328* (F, GH, US); Ambo, *Ferreyra 6912* (GH, USM). LIMA: km. 68, Carretera Central, *Saunders 220,* in part (BM). HUANCAVELICA: Río Mantaro, 70 km. s. of Mejorada, *Hutchison 1689* (GH, UC); entre Pampas y Salcabamba, prov. Tayacaja, *Tovar 3848* (GH, USM). APURIMAC: Quisapata, prov. Abancay, *Vargas 8910* (MO, UC); ca. 10 km. above Pajonal, *West 3676* (GH). CUZCO: Río Sambray, *Mexia 8055* (F, GH, MO, UC, US); Quillabamba, *Stork et al. 10449* (F, GH, UC).

10. **Notholaena mollis** Kze. Linnaea 9: 54. 1834. Type: Playa Ancha, near Valparaiso, Chile, *Poeppig,* LZ, destroyed. FIG. 80.

Rhizome short-creeping, knotted, scales narrow-linear, entire; leaves to 30 cm. tall, petiole usually shorter than the lamina, with one vascular bundle; lamina lanceolate, to tripinnate, ultimate segments small, suborbicular, their lower surface densely covered with whitish to ferrugineous, stellate trichomes; sporangia borne on the vein-ends, margin unmodified, strongly revolute.

Notholaena mollis is amply distinguished by its indument of stellate trichomes, and its tripinnate lamina with small, suborbicular ultimate segments.

Southern Peru and Chile.

On lomas, Arequipa, 100 m.

Specimen examined: AREQUIPA: Mollendo, *Weberbauer 1545* (B).

11. **Notholaena sulphurea** (Cav.) J. Sm. Bot. Voy. Herald 1: 233. 1854. FIG. 81.

Pteris sulphurea Cav. Descr. 269. 1802. Type: Chimapan (Zimapan), Hidalgo, Mexico, *Née,* MA; isotype: F! G!

Cheilanthes Borsigniana Koch, Wochen. Gärtn. Pflanzenkr. 1: 2.

1858. Type: Peru, *Warszewicz*, **B**! photo **GH**.

Notholaena candida var. *lutea* Hook. Sp. Fil. 5: 111. 1864, not *Pteris lutea* Cav. Type: Huánuco, Peru, *Mathews 981*, **K**!

Notholaena sulphurea var. *flava* Kuhn, Abhandl. Ges. Halle 11: 32. 1869. Type: "Peru."

Rhizome short-horizontal, scales lance-ovate, attenuate, with deciduously glandular-ciliate margins; leaves to 20 cm. tall, petiole usually much longer than the lamina, with one vascular bundle; lamina pentagonal, bipinnate-pinnatifid at the base, pinnate-pinnatifid above the basal pinnae, ultimate segments adnate, the lower surface densely yellow to whitish-yellow ceraceous; sporangia borne on the vein-ends, margin thick, otherwise unmodified, somewhat revolute.

Among the three Peruvian species with waxy indument, *N. sulphurea* is easily distinguished by its adnate segments, *N. Stubeliana* and *N. nivea* having stalked ones. The wax is usually yellow but it varies to a very pale yellow.

Mexico to Chile.

Open rocky places, Amazonas to Arequipa, 1500-2500 m.

Maps 21-22. Map 21, *Notholaena Fraseri*. Map 22, *N. nivea*.

Selected specimens: CAJAMARCA: Cantange, Celedín to Río Marañon, *López & Sagástegui 3367* (GH). AMAZONAS: Sunibamba, Utcubamba valley, *Stübel 1048,* in part (B). ANCASH: Caráz, *Weberbauer 3007* (B). HUANUCO: Piedra Grande, *Macbride & Featherstone 2051* (GH, US), *Stork & Horton 9395* (F, UC). LIMA: Mts. back of Lima, *Safford 993* (US); Matucana, *Macbride & Featherstone 426* (US). HUANCAVELICA: Valle de Mantaro, entre Pampas y Salcabamba, *Tovar 3840* (GH, USM). APURIMAC: 80 km. from Abancay, on road to Challhuanca, *Saunders 769* (GH). AREQUIPA: Arequipa, *Rauh P567* (B).

12. **Notholaena Stuebeliana** (Hieron.) Tryon, Rhodora 63: 83. 1961. FIG. 82.

Pellaea dealbata var. *Stuebeliana* Hieron. Hedwigia 48: 225, t. 12, f. 15. 1909. Type: Sunibamba, Dept. Amazonas, Peru, *Stübel 1048,* in part, B!

Rhizome short, erect or decumbent, scales linear, margin entire, brown, oily, concolorous; leaves 10-25 cm. long, petiole as long as, or longer than, the lamina, with one vascular bundle; lamina deltoid to long-triangular, tripinnate to quadripinnate, the lower surface densely white to very pale yellow ceraceous, ultimate segments persistent, mostly orbicular or nearly so; sporangia borne on the terminal ¼ of the vein, margin unmodified.

Peru.

Among boulders and on ledges on shrubby slopes, moist ravines and rocky soil, Cajamarca and Amazonas to Huánuco, 1800-3000 m.

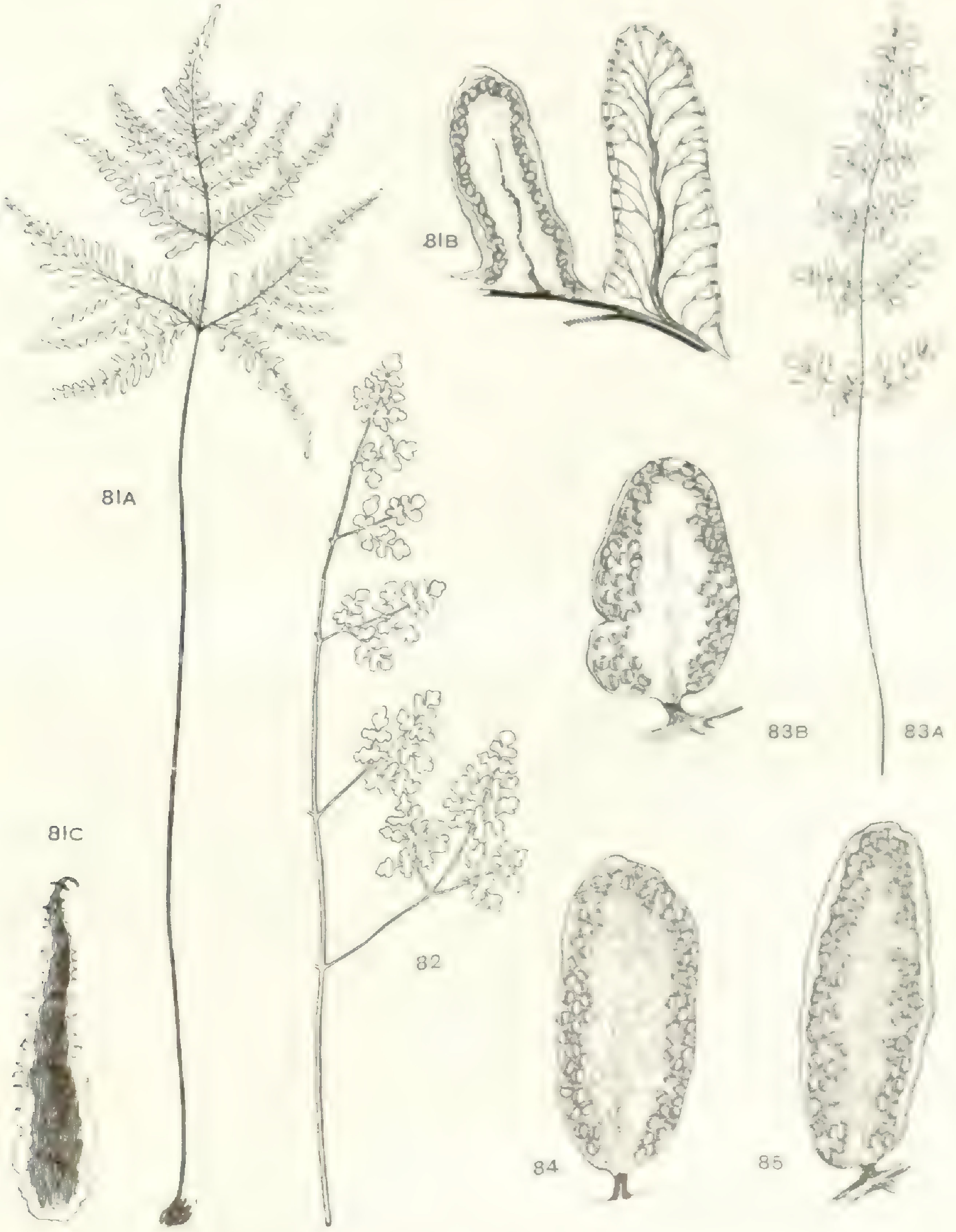
Specimens seen: CAJAMARCA: 40 km. from Cajamarca on road to Chilete, *Correll & Smith P841* (GH, LL, US); Celendín, *López & Sagástegui 3104* (GH). AMAZONAS: Sunibamba, valle Río Utcubamba, *Stübel 1048,* in part (B). LIBERTAD: Camino de las Quishuas, Bolivar, *López & Sagástegui 3288* (GH); Retamas, *López & Sagástegui 3606* (GH). HUANUCO: Mito, *Bryan 192* (F).

13. **Notholaena nivea** (Poir.) Desv. Jour. Bot. Appl. 1: 93. 1813. FIG. 70, MAP 22.

Pellaea nivea (Poir.) Prantl, Bot. Jahrb. 3: 417. 1882.

Rhizome short, erect or somewhat oblique, scales linear-subulate, margin entire; leaves to 30 cm. tall, petiole shorter than the lamina or about equalling it, with one vascular bundle; lamina lanceolate, deltoid-lanceolate to ovate, to tripinnate, the ultimate segments stalked, the lower surface densely yellow or white ceraceous or glabrous; sporangia borne on the terminal ½ to ¼ of the veins, margin unmodified.

This species is a characteristic fern of the Altiplano and the rocky, semi-arid valleys to the east and west. The four varieties all occur in Peru and often two may be found growing in the same habitat.



FIGS. 81-85. Fig. 81. *Notholaena sulphurea:* A. leaf, × ½, Mexico, *Meyer & Rogers [illegible]882*, MO; B, segments, lower surface, × 4½, *idem;* C, rhizome scale, × 9, *idem.* Fig. 82. *N. Stuebeliana:* lamina (½), × 1, Peru, *Correll & Smith P841*, GH. Fig. 83. *N. nivea* var. *nivea:* A, leaf, × ½, Bolivia, *Buchtien [illegible]*, MO; B, segment, lower surface, × 4½, *idem.* Fig. 84. *N. nivea* var. *oblongata:* segment, lower surface, × 4½, Argentina, *Lossen 242*, MO. Fig. 85. *N. nivea* var. *tenera:* segment, lower surface, × 4½, Argentina, *Venturi 10639*, MO.

Colombia to Argentina and Brazil.

Rocky hillsides and crevices of rocks, Cajamarca to Puno and Arequipa, 1200-3800 m.

KEY TO VARIETIES

a. Indument white. .... b.

  b. Ultimate segments suborbicular to broadly oblong, the terminal one often lobed, petiole castaneous, rhizome scales often strongly crisped. .... 13a. var. *nivea*

  b. Ultimate segments oblong and entire, or subdeltoid and trilobate, the terminal one commonly simple, petiole bright castaneous, rhizome scales not strongly crisped. .... 13b. var. *oblongata*

a. Indument yellow or none. .... c.

  c. Indument none. .... 13. var. *tenera*

  c. Indument yellow. .... 13d. var. *flava*

13a. **Notholaena nivea** var. **nivea.** FIGS. 70, 83.

Pteris nivea Poir. Lam. Encycl. 5: 718. 1804. Type: Peru, *Joseph de Jussieu* (Herb. Jussieu no. 1047), P! photo GH.

Ecuador to w. Argentina.

Libertad to Puno and Arequipa.

Selected specimens: LIBERTAD: Otuzco to Huamchirco, *Ferreyra 2987* (USM); Cerro Chologday, prov. Otuzco, *Sagástegui 79* (GH). ANCASH: Caráz, *Weberbauer 3009* (B); Chiquián, *Cerrate 240, 564, 2106* (USM). HUANUCO: prov. Huánuco, *Ruiz 45* (B); Huánuco, *Macbride 3207* (F). LIMA: San Mateo, *Ferreyra 7028* (GH, USM); Oroya RR., *Safford 990* (GH, NY, P, US); Río Blanco, *Killip & Smith 21561* (GH, NY, US). JUNIN: Tarma, *Killip & Smith 21812* (F, NY, US); Vilcabamba, *Tryon & Tryon 5422* (F, BM, MO, U, US, USM). HUANCAVELICA: Huancavelica, *Stork & Horton 10823* (F, UC); between Colcabamba and Paucarbamba, *Tovar 2110* (GH, USM). AYACUCHO: Ayacucho, *West 3642* (UC). APURIMAC: Andahuaylas, *Stork & Horton 10718* (F, UC). CUZCO: Saxihuaman, *Tryon & Tryon 5344* (BM, F, GH, MO, U, US, USM), *Coronado 158* (GH, UC). PUNO: Baja Isla, Lake Titicaca, *Mexia 7788* (F, GH, MO, UC); Tequeña, *Aguilar 133* (USM). AREQUIPA: Arequipa, *Pennell 13245* (F); El Misti, *D. Stafford 572* (BM).

13b. **Notholaena nivea** var. **oblongata** Griseb. Abh. König. Ges. Wiss. Gött. 24(Symb. Fl. Argent.): 342. 1879. Type: Salta, Argentina, *Hieronymus & Lorentz 142* and *161*, B! photo GH. FIG. 84.

Peru, Argentina and Brazil.

Huánuco to Cuzco.

Specimens seen: HUANUCO: Chavenillo, *Woytkowski 1028* (UC).

APURIMAC: Andahuaylas, *Herrera 1498*, in part (GH). CUZCO: Cuzco, *Soukup* (USM), *76* (GH). PUNO: Macusani, *Lechler 1830* (B).

13c. **Notholaena nivea var. tenera** (Hook.) Griseb. Abh. König. Ges. Wiss. Gött. 24(Symb. Fl. Argent.): 342. 1879. FIG. 85.

Notholaena tenera Hook. Curtis, Bot. Mag. t. 3055 & text. 1831. Type: Spec. cult, ex Mendoza, Argentina, *Gillies*, K! photo GH.

Pellaea tenera (Hook.) Prantl, Bot. Jahrb. 3: 417. 1882.

Pellaea peruviana Copel. Univ. Cal. Publ. Bot. 19: 302. 1941. Type: Abancay region, Apurímac, Peru, *pupils of V. Santander C.* UC!

A collection by Soukup (*1488*, USM) is said to be from Cerro Jeronimo, a loma near Lima, but this represents the only occurrence of *Notholaena nivea* on a loma and the record needs to be confirmed.

Peru to Argentina.
Libertad to Puno.

Selected specimens: LIBERTAD: arriba de Casmiche, prov. Otuzco, *López et al. 3962* (GH). ANCASH: Cerro de Huasta, *Cerrate 2456* (GH, USM). HUANUCO: between Huanucay and Ambo, *Ferreyra 6566* (USM). LIMA: Matucana, *Macbride & Featherstone 82* (F, GH); entre Matucana y San Mateo, *Ferreyra 5306* (GH, USM). JUNIN: Palca, *Correll & Smith P758* (GH). HUANCAVELICA: Mejorada, *Tovar 1000* (GH, USM). CUZCO: Cuzco, *Tryon & Tryon 5353* (BM, F, MO, U, US, USM); Yucay, *Coronado 142* (GH, UC). PUNO: Tequeña, Feb. 19, 1948, *Aguilar* (USM).

13d. **Notholaena nivea var. flava** Hook. Sp. Fil. 5: 112. 1855. Type: ?

Acrostichum tereticaulon Desv. Ges. Naturf. Freunde Berl. Mag. 5: 310. 1811. Type: perhaps Peru, *Dombey*, P! photo GH.

Notholaena chrysophylla Kl. Allg. Gartenzeit. 23: 265. 1855. Type: spec. cult. ex Peru, *Warszewicz*, B!

Pellaea flavens (Sw.) C. Chr. Ind. Fil. 480. 1906.

Colombia to Argentina and Brazil.
Cajamarca to Cuzco.

Specimens seen: CAJAMARCA: Between San Marcos and Cajabamba, *Correll & Smith P908, P912* (GH). HUANUCO: Huánuco, *Pearce 54* (BM); Piedra Grande, *Macbride & Featherstone 3706* (F, US). HUANCAVELICA: Valle de Mantaro, entre Pampas y Salcabamba, *Tovar 3847* (GH, USM). CUZCO: Potrero, *Tryon & Tryon 5378* (BM, F, MO, U, US, USM), *Coronado 111* (GH, UC, US), *Vargas 1807* (GH).

17. PELLAEA Link, Fil. Sp. Hort. Bot. Berol. 59. 1841, conserved name. Type: *Pteris atropurpurea* L. = *Pellaea atropurpurea* (L.) Link.

Terrestrial, the rhizome moderately stout and compact to slender and creeping, scaly, bearing the leaves in a cluster or spaced; leaves small to large, 1- pinnate to quadripinnate, glabrous or nearly so, veins free; sporangia borne on the apical ¼ of the vein or at its tip, covered by an indusium which is formed from the reflexed, modified margin, paraphyses absent. — About 25 species in America.

Tryon, A. F. A revision of the fern genus Pellaea section Pellaea. Ann. Mo. Bot. Gard. 44: 129-193. 1957.

The treatment of this genus has been adapted by Alice F. Tryon from the monograph cited above. The American species are well represented in the southwestern United States and Mexico. The three Peruvian species have a Cordilleran distribution, ranging from Texas and Mexico to Bolivia and Argentina. They are especially common in the Altiplano and adjacent valleys, in dry, rocky hillsides or among rocks of old walls.

KEY TO SPECIES

a. Petiole and rachis atropurpureus to black in color; the pinnae pinnate and mostly ternately divided. .... 1. *P. ternifolia*
a. Petiole and rachis ruddy-brown to straw colored; the pinnae usually bi-quadripinnate with more than 3 segments. .... b.
  b. Rhizome moderately stout, compact; scales at the very base of the petiole and those of the buds tan, concolorous. .... 2. *P. sagittata*
  b. Rhizome slender, cord-like, creeping; scales at the very base of the petiole and those of the buds bicolorous, tan to dark brown, the central portion often lustrous, sclerotic. .... 3. *P. ovata*

1. **Pellaea ternifolia** (Cav.) Link, Fil. Sp. Hort. Bot. Berol. 59. 1841, var. **ternifolia.** FIG. 86, MAP 23.

Pteris ternifolia Cav. Descr. 266. 1802. Type: *Née*, Peru, MA; isotype: F!

Pteris peruviana Poir. in Lam. Encycl. Méth. Bot. 5: 718. 1804. Type: *Joseph de Jussieu*, Peru, (Herb. Jussieu no. 1334A), P! photo GH.

Rhizome moderately stout, elongate, decumbent, multicipital, scales of the rhizome (and those at the base of the petiole) straight or falcate, bicolorous with a slender sclerotic stripe usually narrower than the border, the margin at the scale base entire, dentate above, the apex attenuate, filiform; leaves 4-50 cm. long, stiff, erect, petiole and rachis plane on the upper surface or sulcate, atropurpureous or black, lamina linear to narrowly lanceolate, once pinnate, pinnae ternate or entire, sessile or subsessile, without pinna-rachises; indusium formed by the enrolled somewhat membranaceous segment margin, spores with a sparse, scarcely prominent, rugose exospore, 64 per sporangium.

This species is characterized by the blackish petioles and ternate form of the pinnae. It has the widest distribution of the New World species of Pellaea, occurring along the Cordillera from Arizona to Argentina and in Hispaniola and the Hawaiian Islands. Some specimens from high altitudes in Bolivia and Argentina have been segregated as *Pellaea Weddelliana* on the basis of the nearly simple pinnae and almost concolorous scales but they are not sufficiently distinct or consistent in these characters to warrant recognition.

Southwestern United States to Nicaragua; Hispaniola; Venezuela to Colombia to Argentina; Hawaiian Islands.

In crevices of igneous rocks or in Inca walls, in sun and semi-shade, Cajamarca and Amazonas to Puno and Arequipa, 1800-4000 m.

Selected specimens: CAJAMARCA: cumbre El Gavilan, Cajamarca, *Ferreyra 3269* (USM); between Llacanora and Namora, *Correll & Smith P888* (GH). AMAZONAS: Carrizal, *Stübel 1025* (B). LIBERTAD: n. of Cachicadán, prov. Santiago de Chuco, *Stork & Horton 9997* (F, UC); Huaranchal, *López et al. 2691* (GH). ANCASH: Chiquián, *Cerrate 622, 786* (USM), *Ferreyra 6273* (USM). HUANUCO: near Panao, *Asplund 13679* (US); Mito, *Bryan 198* (F). LIMA: cerca Tupe, *Cerrate 1089* (USM); Matucana, *Macbride & Featherstone 286* (F). JUNIN: Tarma, *Killip & Smith 21817* (NY, US); Huacapistana, *Tryon & Tryon 5424* (BM, F, MO, U, US, USM). HUANCAVELICA: Conaica, *Tovar 976* (GH, USM). AYACUCHO: km. 45, Nasca to Puquio, *Correll & Smith P171A* (LL), km. 126, Nasca to Puquio, *Correll & Smith P158* (LL). APURIMAC: 2 km. n. of Andahuaylas, *Stork & Horton 10720* (F, UC). CUZCO: Ollantaytambo, *Cook & Gilbert 399, 553, 693* (US); Yucay, *Coronado 145* (GH, UC); Saxihuaman, above Cuzco, *Tryon & Tryon 5358* (BM, F, MO, U, US, USM). PUNO: Juliaca, *R. S. Williams 2633* (GH, NY, US); Azángaro, *Lechler 1746* (B), *Weberbauer 481* (B). AREQUIPA: Tiabaya, *Pennell 13075* (B, F, GH, NY, US); El Misti, *Cárdenas & Rodriguez 14* (F).

2. **Pellaea sagittata** (Cav.) Link, Fil. Sp. Hort. Bot. Berol. 60. 1841, var. **sagittata.** FIG. 87.

Pteris sagittata Cav. Descr. Pl. 267. 1802. Type: *Née*, Cerro de Guadeloupé, Mexico, MA.

Rhizome moderately stout, compact, decumbent, multicipital, scales straight or nearly so, concolorous, tan to rust-colored, elongate, lanceolate-triangular, usually cordate, the margins irregularly dentate, the apex filiform, more or less tortuous; leaves 16-78 cm. long, erect, stiff, scales of the base of the petiole and the buds straight, concolorous,

FIGS. 86-88. Fig. 86. *Pellaea ternifolia* var. *ternifolia:* A, rhizome and attached leaf, × ½, Colombia, *Killip & Smith 18751*, GH; B, fertile ultimate segment, enlarged, *idem*. Fig. 87. *P. sagittata* var. *sagittata:* rhizome and attached leaf, × ½, Guatemala, *Skutch 805*, GH. Fig. 88. *P. ovata:* A, lamina, × ⅓, Peru, *Vargas 1051*, GH; B, rhizome, × ½, *idem*.

tawny, broadly ovate-lanceolate, cordate or pseudopeltate, the margin erose, the apex filiform, tortuous, petiole and rachis convex or plane on the upper surface, puberulous, the rachis straight or somewhat flexuous, straw to ruddy tan or mottled becoming darker with age, lamina elongate ovate-triangular or rhomboid, 1-pinnate or bipinnate, rarely tripinnate, the pinnae ascending at acute angles to the rachis, pinnae entire or divided into 3-18 segments, long-stalked; indusium formed by the enrolled, partly membranaceous segment margin, spores with sparse, prominent rugae, 32 per sporangium.

This species is distinguished by the light colored petioles, the sagittate form of the segments and straight rachises. All of the South American specimens have 32 spores per sporangium, in which they differ from the cordate segmented var. *cordata* (Mexico to Texas) which has 64 smaller spores per sporangium. The South American plants seem to be apogamous derivatives of var. *cordata*.

Central Mexico to Guatemala; Colombia to Bolivia.

On dry banks, in open sun or shade, among limestone rocks or stone fences, south-central Peru, Pasco to Cuzco, 1700-3000 m.

Selected specimens: PASCO: entre Salcahupan y Cerro de Pasco, *Ferreyra 6621* (GH, USM). LIMA: Matucana, *Macbride & Featherstone 422* (F, GH). JUNIN: Huacapistana, *Tryon & Tryon 5431* (BM, F, GH, MO, U, US, USM); Carpapata, *Cerrate 2798* (GH, USM). HUANCAVELICA: Conaica, *Tovar 978* (USM); entre Colcabamba y Paucarbamba. *Tovar 2072* (USM). APURIMAC: Upper Río Marino, prov. Abancay. *Stork et al. 10648* (F, UC). CUZCO: Urubamba, *Cook & Gilbert 254* (GH), *254a* (US); valle de Urubamba, *Herrera 1195* (F, US).

3. **Pellaea ovata** (Desv.) Weath. Contrib. Gray Herb. 114: 34. 1936. FIG. 88, MAP 24.

Pteris ovata Desv. Mém. Soc. Linn. Paris 6: 301. 1827. Type: Peru, Herb. Desvaux, P! photo GH, UC.

Rhizome slender, cord-like, creeping, dichotomously branched, scales of the rhizome (and those at the base of the petiole) straight or somewhat falcate, bicolorous, the sclerotic central portion lustrous (scales on the old portion of the rhizome nearly wholly sclerotic), the margin pectinate to erose-serrulate, the apex filiform, more or less tortuous, leaves 10-125 cm. long, straight or frequently twining, subscandent, petiole and rachis convex or plane on the upper surface, the rachis strongly flexuous, straw to ruddy brown becoming gray with age, lamina elongate triangular, bi- to quadripinnate, usually tripinnate, the pinnae descending from the rachis, pinnae divided into 5-60 segments, long stalked; indusium formed by the enrolled, somewhat membranaceous segment margin, spores with a prominent light brown, rugose exospore, 32 per sporangium.

Pellaea ovata is unique among most rock ferns in its slender long-creeping rhizome and usually strongly flexuous rachises with descending pinnae. Specimens from southern Texas and northern Mexico have 64 spores in the sporangium while those from central and southern Mexico, Hispaniola and South America have 32.

Southern Texas to Nicaragua; Hispaniola, Jamaica; Venezuela to Colombia to northern Argentina.

Subscandent, in open sun, brushy savanna, among limestone rocks, on shaded banks or stone fences, Cajamarca to Puno, 1200-2850 m.

Selected specimens: CAJAMARCA: 52 km. w. of Cajamarca on road to Chilete, *Correll & Smith P839* (GH). LIBERTAD: Retamas, *López & Sagástegui 3608* (GH); Sinsicap, prov. Otuzco, *López et al. 2270* (GH). HUANUCO: entre Ambo y Huánuco, *Ferreyra 9232* (GH, USM); Muña, *Bryan 438* (F); Acomayo, Feb. 1940, *Ridoutt* (GH, USM). JUNIN: 2 km. arriba de Huacapistana, *Ferreyra 425* (GH, USM); Huacapistana, *Tryon & Tryon 5423* (BM, F, GH, MO, U, US, USM). HUANCAVELICA: La Mejorada, *G. Kunkel 452* (GH). APURIMAC: Andahuaylas, *Herrera 1497* (F, GH); w. of Pincos, prov. Andahuaylas, *Stork & Horton 10712* (F, UC). CUZCO: San Miguel, Urubamba valley, *Cook & Gilbert 1765* (US); Yucay, *Soukup 754* (F, GH), *Vargas 1051* (GH). PUNO: Sandia, *Weberbauer 841* (B).

18. **DORYOPTERIS** J. Sm. Jour. Bot. Hooker, 4: 162. 1841. Type: *Pteris palmata* Willd. = *Doryopteris palmata* (Willd.) J. Sm. = *Doryopteris pedata* var. *palmata* (Willd.) Hicken.

Terrestrial, the rhizome small to moderately stout, erect to decumbent or creeping, scaly, bearing the leaves in a crown or loose cluster; leaves small, the lamina pedate, deeply lobed to tripinnatifid, glabrate, veins free or anastomosing; sporangia borne on a continuous or interrupted marginal commissure, covered by an indusium which is formed from the reflexed and modified margin, paraphyses absent. — 23 species in America.

Tryon, R. A revision of the genus Doryopteris. Contrib. Gray Herb. 143. 1942.

Doryopteris is distinguished by its black or atropurpureous petioles, pedate laminae and usually long-stalked sporangia borne in a continuous marginal line covered by an

MAPS 23-26. Map 23, *Pellaea ternifolia* var. *ternifolia*. Map 24, *P. ovata*. Map 25, *Doryopteris crenulans* (northern dot), *D. lomariacea* (central dot), *D. Lorentzii* (southern dots). Map 26, *Saffordia induta*.

indusium formed from the greatly modified margin. None of the five species in Peru is common; the genus is primarily one of eastern Brazil and diminishes in numbers through Argentina and Bolivia. The region along the eastern side of the Andes in the Department of Cuzco and southeastward is the center in Peru and the area in which species new to the country will most probably be found.

KEY TO SPECIES

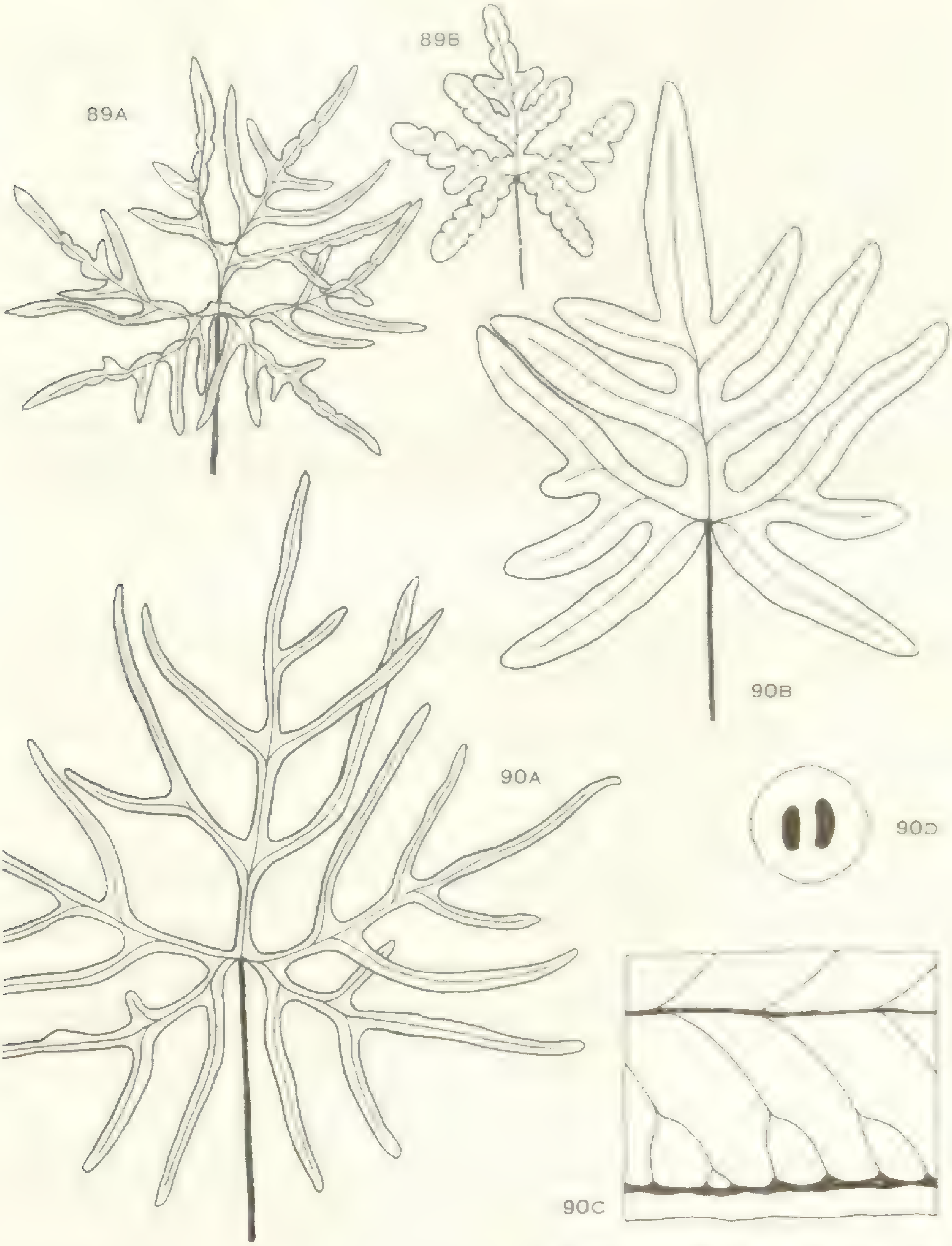
- a. Venation free, single areolae present by rare exception. .... b.
  - b. Petiole sulcate to wing-angled on the upper side, at least toward the base of the lamina, with one vascular bundle. .... 5. *D. concolor*
  - b. Petiole terete or subterete, with two vascular bundles at least toward the base. .... c.
    - c. Fertile lamina usually with numerous ultimate segments, the pinnae and primary segments surcurrent and, except the basal pair, also decurrent, the bases forming wings along the rachis that are broad at their top and bottom and narrowed in their middle. .... 1. *D. crenulans*
    - c. Fertile lamina often with few ultimate segments, the pinnae and primary segments adnate or slightly surcurrent and, except the basal pair, also decurrent, forming wings along the rachis that have nearly parallel sides. .... 2. *D. lomariacea*
- a. Venation completely areolate or with areolae only along the midnerves of the segments, petiole with one vascular bundle. .... d.
  - d. Fertile and sterile laminae with partially areolate venation, the areolae mostly along the midnerves, proliferous buds not present at the base of the lamina. .... 3. *D. lorentzii*
  - d. Fertile and sterile laminae with completely areolate venation, proliferous buds present at the base of the lamina. .... 4. *D. pedata*

1. **Doryopteris crenulans** (Fée) Christ, Schwacke, Pl. Nov. Mineiras 2: 26. 1900. FIG. 89, MAP 25.

Pellaea crenulans Fée, Crypt. Vasc. Brésil 2: 27, t. 87, f. 3. 1872-73. Type: Tijuca, Brazil, *Glaziou 5345*, fragment "ex Fée" NY!; isotype: P, photo GH, GH!

Rhizome scales and those of the leaf buds long and narrow, the cells of the hyaline borders (or of the wholly hyaline scale) mostly three or more times as long as broad; petiole usually densely and minutely verrucose, rarely smooth, with two vascular bundles; fertile and sterile leaves quite dimorphic, coriaceous, the sterile to 35 cm., the fertile to 50 cm. tall, ultimate segments numerous, with free venation, the pinnae and primary segments surcurrent, and, except the basal pair, decurrent, the bases forming wings along the rachis that are broad at the top and bottom and narrowed in the middle; soral lines broken by all or nearly all of the sinuses.

Doryopteris crenulans is distinguished by its free venation, essentially terete petiole with two vascular bundles, the rather strongly dimorphic fertile and sterile laminae, the pinna or primary segment bases that form wings along the rachis that are narrowed in the middle and the soral lines that are broken at most of the sinuses.



FIGS. 89-90. Fig. 89. ***Doryopteris crenulans:*** A, fertile lamina, × ½, Bolivia, *Buchtien 7038*, US; B, sterile lamina, × ½, Brazil, ***Reiss 23***, GH. Fig. 90. ***D. lomariacea:*** A, fertile lamina, × ½, Brazil, *L. B. Smith* [illegible], GH; B, sterile lamina, × ½, Brazil, ***Kunert 26***, US; C, venation and receptacle of fertile segment, × 5, *Smith* [illegible], GH; D, vascular bundles near base of petiole, enlarged, *idem*.

Peru and Bolivia; southern Brazil.

On hillside, in humus and clay soil, Cajamarca, 3200 m.

Specimens seen: CAJAMARCA: Socota, *Stork & Horton 10127* (F, UC, US).

2. **Doryopteris lomariacea** Kl. Linnaea 20: 343. 1847. Type: British Guiana, *Schomburgk 1197;* isotypes: BM! K! FIG. 90, MAP 25.

Rhizome creeping, its scales and those of the leaf-buds long and narrow, the cells of the hyaline borders (or of the wholly hyaline scales) mostly three or more times as long as broad; petiole usually smooth, with two vascular bundles; fertile and sterile leaves coriaceous, strongly dimorphic, the sterile to 50 cm., the fertile to 120 cm. tall, ultimate segments 5 to several, less often numerous, with free venation, the pinnae and primary segments surcurrent and, except the basal pair, also decurrent, forming wings along the rachis that have essentially parallel sides; soral lines continuous around the sinuses.

This species is similar to the preceding in its free venation, the terete petiole with two vascular bundles and the strongly dimorphic fertile and sterile laminae, but differs in the wings along the rachis formed by the bases of the pinnae and primary segments having essentially parallel sides and the soral lines continuous around the sinuses.

Southern Brazil and Paraguay; Peru; British Guiana.

Locally wet places, Junín.

Specimens seen: JUNIN: Eneñas, *Killip & Smith 25709* (NY, US).

3. **Doryopteris Lorentzii** (Hieron.) Diels, Engl. & Prantl, Nat. Pfl. 1(4): 270. 1899. **FIG. 91, MAP 25.**

Pellaea Lorentzii Hieron. Bot. Jahrb. 22: 392. 1896. Lectotype: Córdoba, Argentina, *Lorentz 19,* B! photo GH.

Rhizome scales and those of the leaf buds usually ovate-lanceolate, the cells of the hyaline borders about as long as broad; petiole smooth or slightly pubescent at the top, with one vascular bundle; fertile and sterile leaves moderately dimorphic, moderately coriaceous, the sterile to 18 cm., the fertile to 35 cm. tall, ultimate segments numerous, with areolae along the midnerves, the veins free toward the margin, remotely crenate, the sinuses black and semi-sclerotic; soral lines broken by the sinuses.

Doryopteris Lorentzii is distinguished by its partially areolate venation, the areolae being commonly confined to the area along the midrib. The petiole is terete or rarely sulcate toward the apex and has one vascular bundle. The sinuses are usually black and semi-sclerotic.

Peru to Argentina and southern Brazil.

Rocky places, Cuzco, 1200-2500 m.

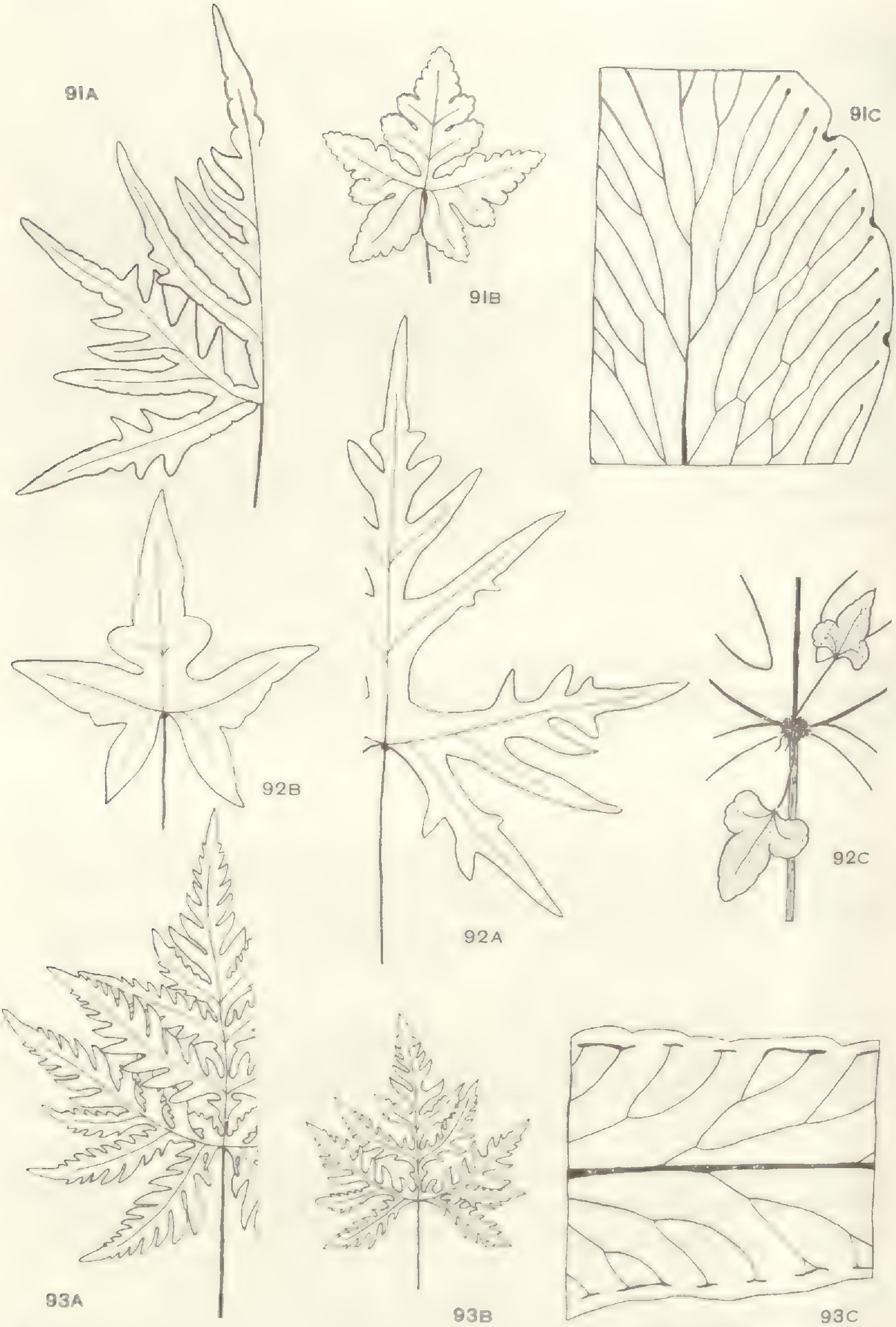
Specimens seen: CUZCO: Potrero, *Coronado 115* (GH, UC, US), *Tryon & Tryon 5377* (BM, F, MO, U, US, USM); Yucay, *Soukup 921* (F); Dist. Santa Ana, *Herrera 871a* (US); Santa Ana, *Cook & Gilbert 1479* (US, in part); Valle de Lares, *Herrera 1635* (US); Machu-Picchu to Quillabamba, *Mexia 8053a* (F, UC, in part).

4. **Doryopteris pedata** (L.) Fée, var. **palmata** (Willd.) Hicken, Rev. Mus. Plata 15: 253. 1908. FIG. 92.

Pteris palmata Willd. Sp. Pl. 5: 357. 1810. Type: Caracas, Venezuela, *Bredemeyer*, (Herb. Willd. 19957), B! photo GH! NY! US!

Rhizome scales and those of the leaf buds usually ovate-lanceolate, the cells of the hyaline borders about as long as broad; petiole usually pubescent, with one vascular bundle; fertile and sterile leaves moderately dimorphic, moderately coriaceous, the sterile to 37 cm., the fertile to 40 cm. tall, both with proliferous buds at the base of the lamina, ultimate segments several to many, with areolate venation; soral lines usually broken by the sinuses.

This variety is easily identified by the proliferous buds that are borne at the base of the lamina, one on each side of the petiole apex. The buds develop as the leaf ages and old leaves that have come to rest on the ground have young plants developed from them. These continue to grow and are an effective means of reproducing the species locally. Rarely some leaves of a plant lack buds, and in young leaves they are rather inconspicuous. The petiole is usually plane on the upper side, at least in part, and the sinuses are only occasionally blackish and are cartilaginous, not sclerotic. The closely related var. *multipartita* (Fée) Tryon is known from Bolivia; it may be distinguished by the lack of proliferous buds, the more divided lamina and the spores which lack perispore; in var. *palmata* a perispore is present. The completely areolate venation separates var. *multipartita* from *D. Lorentzii*. *Doryopteris nobilis* also is a marginal species distinguished by large laminae, usually with buds at the base of the lamina as in *D. pedata* var. *palmata* but with the sterile tips of the segments crenate or crenulate with



FIGS. 91-93. Fig. 91. *Doryopteris Lorentzii:* A, fertile lamina, × ½, Bolivia, *Buchtien 3397*, US; B, sterile lamina, × ½, Argentina, *Maldonado 402*, GH; C, venation of sterile segment, × 5, Argentina, *Vattuone & Bianchi 165*, US. Fig. 92. *D. pedata* var. *palmata:* A, fertile lamina × ½, Bolivia, *Rusby 135*, NY; B, sterile lamina × ½, Costa Rica, *Skutch 2746*, US; C, young plant from proliferous bud at base of lamina, × 5, cult. *U. S. Bot. Gard.* in 1884, US. Fig. 93. *D. concolor* var. *concolor:* A, fertile lamina, × ½, Brazil, *Wacket*, US; B, sterile lamina, × ½, Peru, *Vargas 1709*, GH; C, venation and receptacles of fertile segment, × 10, El Salvador, *Calderón 1714*, US.

ascending teeth; in *D. Lorentzii* and *D. pedata* var. *palmata* the sterile tips are entire or have spreading teeth.

Venezuela to Colombia; south to Bolivia and north to Mexico.

Rocky woods, Cajamarca and Cuzco, 1200-2200 m.

Specimens seen: CAJAMARCA: prov. Hualgayoc, *Soukup 3814* (US). CUZCO: Potrero, *Coronado 114* (GH, UC, US), *Tryon & Tryon 5469* (BM, F, GH, MO, U, US, USM), *Vargas 1705* (GH); Torontoy, *Herrera 1304* (US); Yucay, *Soukup 920* (F); Colpani, *Cook & Gilbert 1062* (GH).

5. **Doryopteris concolor** (Langsd. & Fisch.) Kuhn, v. d. Decken, Reisen Ost-Afrika 3(3): 19. 1879. var. **concolor.** FIG. 93.

Pteris concolor Langsd. & Fisch. Ic. Fil. 19, t. 21. 1810. Type: "Archipelagi Marquesas; insula Nucahiva"; isotype: (Herb. Willd. 19961-1), B! photo GH.

Rhizome scales and those of the leaf buds usually ovate-lanceolate, the cells of the hyaline borders about as long as broad; petiole wing-angled or sulcate on the upper side, glabrous or glabrate, with one vascular bundle; fertile and sterile leaves similar, herbaceous, the sterile to 15 cm. the fertile to 35 cm. tall, ultimate segments very numerous, with free venation; soral lines usually broken by the sinuses.

The American *Doryopteris concolor* all belongs to var. *concolor*, the other variety, var. *Kirkii*, being in Africa, India and Ceylon. The venation is free which distinguishes it from the two preceding species and the single vascular bundle in the petiole will distinguish it from the first two, as does the sulcate or wing-angled petiole. The texture of the lamina is herbaceous while in all of the other species it is coriaceous.

Tropical America.

Rocky places and clay banks, Cajamarca to Cuzco, 750-2000 m.

Selected specimens: CAJAMARCA: Jaén, Feb. 17, 1954, *R. Cerrón* (GH, UC, US). SAN MARTIN: Tarapoto, *L. Williams 5451* (F, GH), *Spruce 4045* (K). CUZCO: Valley of the Vilcanota, *Mexia 8053* (GH, MO, UC, US); Santa Ana, *Cook & Gilbert 1512, 1553* (US); Potrero, *Coronado 113* (GH, UC, US), *Tryon & Tryon 5375* (BM, F, GH, MO, U, UC, US, USM).

19. **SAFFORDIA** **Maxon**, Smiths. Misc. Coll. 61(4): 1. 1913. Type: *Saffordia induta* Maxon.

Terrestrial, the rhizome rather small, erect, scaly, bearing the leaves in a rosette or cluster; leaves small, the lamina pedate, bipinnatifid, densely scaly beneath, glabrous above, veins anastomosing; sporangia borne along and between the veins in a narrow band close to the unmodified margin, indusium and paraphyses absent. — A Peruvian genus of 1 species.

Ballard, F. Saffordia induta, Hook. Ic. Pl. t. 3599 & text. 1962.

The genus was long known only from the original collection made in Lima by Safford in 1892; it was recollected at about the same place in 1954 and by 1959 its range had been extended to La Libertad and Cajamarca.

Saffordia induta Maxon, Smiths. Misc. Coll. 61(4): 2, t. 1-2. 1913. Type: Along the Arroya (La Oroya) Railway, in the mountains back of Lima (probably near Matucana), Peru, *Safford 989*, US!; isotype: B! GH! K! UC! FIG. 95, MAP 26.

Rhizome scales subulate to lance-subulate, light brown to brown, concolorous, the margins toothed; leaves ca. 15-30 cm. long, petiole deciduously scaly, reddish-brown to nearly atropurpureous, longer than the blade, with one vascular bundle, the scales at its base lanceolate to ovate-lanceolate, reddish-brown or pinkish, the margins toothed to subfimbriate; blade more or less suborbicular, the scales (beneath) densely appressed-imbricate, deltoid-ovate to long-deltoid, prominently fimbriate.

The pink color present in the scales at the base of the petiole is a unique one among ferns. This color was especially evident among the many living plants at Kew (1960) which had been grown from spores sent by Mr. S. G. E. Saunders. Young plants among these cultures had the smallest leaves nearly orbicular, larger ones were oblong-cordate to long deltoid-sagittate, and the largest were 3-lobed. Mr. Saunders has written me that it has grown well for him in a pot in Lima and that "When dry, the leaves curl inward like a clenched fist, and conceal all of the green upper surface; after watering they open again."

Peru.

Among rocks, Cajamarca, Libertad and Lima, 2200-2900 m.

Specimens seen: CAJAMARCA: between Santiago and Guzmango, prov. Contumazá, *Sagástegui 2936* (GH); between Cascas and Contumazá, *López et al. 3683* (GH). LIBERTAD: Huaranchal, prov. Otuzco, *Sagás-*

tegui 205 (GH). LIMA: Mountains back of Lima, *Safford 989* (B, GH, K, UC, US); km. 68, Carretera Central, dist. Surco, *Saunders 218* (BM); Matucana, *Rauh P186* (B).

20. ADIANTUM L. Sp. Pl. 2: 1094. 1753; Gen. Pl. 485. 1754. Type: *Adiantum Capillus-Veneris* L. FIG. 94.

Terrestrial, the rhizome small and suberect, stout and short-creeping, or slender and long-creeping, scaly, bearing the leaves in a cluster or well spaced; leaves small to very large, pinnate (1-pinnate to 6-pinnate) or helicoid (in *A. patens*), usually glabrous, less often sparingly scaly, pubescent or ceraceous beneath, veins free; sorus marginal, not paraphysate, the sporangia borne along (or also between) the vein-tips which extend into the indusium which is formed from a reflexed, modified lobe. — About 75 species in South America.

Kramer, K. U. A contribution to the fern flora of French Guiana, (Adiantum). Acta Bot. Neerland. 3: 481-486. 1954.

FIG. 94. *Adiantum Capillus-Veneris*, sea cliffs at Miraflores (Lima).

Adiantum is one of the best defined genera of ferns, the sporangia-bearing veins that enter the marginal indusium being a distinctive feature. Also, the aspect of the leaves is characteristic, although variable and difficult to define, but once a few species of the genus are known others can readily be placed there.

The genus is widely distributed in Peru and is one of the common ones both in number of species and individuals. Most of the species fall into a few rather well marked geographic groups. One group, species 10-24, is characteristic of the Amazon Basin and the lower elevations of the eastern slopes of the Andes. Another, species 1-8 and 25, is characteristic of the eastern slopes of the Andes and their valleys. A third, species 33-35, of the valleys and sheltered places of the Altiplano and the higher elevations of the eastern and western Andean valleys. A fourth, species 31 and 38, occurs primarily on the costal lomas, although also present in the Altiplano. Finally, a single species, 30. *A. Capillus-Veneris*, is probably an escape from cultivation; with a single exception it grows near Lima.

KEY TO SPECIES

a. Ultimate segments all sessile or subsessile, or rarely some basal ones short-stalked. .... b.

b. Lateral ultimate segments nearly symmetrical, at least in their apical half, in bipinnate laminae the terminal pinna much larger than the few laterals and usually broadest at the base. .... c.

c. One long sorus on each edge of the pinna, or pinnule, or rarely only on the upper edge, or a few short ones in addition. .... d.

d. Rachis glabrous, lamina 1-pinnate the pinnae usually opposite. .... 5. *A. macrophyllum*

d. Rachis pubescent-scaly or scaly, pinnae alternate, rarely subopposite. .... e.

e. Rhizome scales dull, rachis pubescent-scaly or scaly on all sides, rarely glabrate in *A. Poeppigianum*. .... f.

f. Rachis densely scaly, the scales freely ciliate, pinnae with long brown trichomes beneath, lamina 1-pinnate. .... 6. *A. scalare*

f. Rachis moderately pubescent-scaly, the scales mostly ciliate only at the expanded base, pinnae glabrous or slightly scaly beneath, lamina 1- to bipinnate. .... g.

g. Dark color of the segment-stalk definitely entering the base of the segment beneath, midvein distinct to the apex. .... 7. *A. Poeppigianum*

g. Dark color of the segment-stalk not or hardly entering the base of the segment, midvein indistinct or lacking in the apical half. .... 8. *A. lucidum*

e. Rhizome scales iridescent, rachis pubescent-scaly on the upper side, glabrous below, lamina 1- to bipinnate. .... 9. *A. alarconianum*

c. Several oblong or arcuate sori on each edge of the pinna or pinnules, or only on the upper edge, lamina 1- to bipinnate. .... h.

h. Segments dull, usually glaucous, beneath, the sterile ones or portions evenly serrate. .... i.

i. Rhizome short-creeping, usually nodose, with the scales appressed, the petiole bases approximate; lamina bipinnate, segments with usually numerous simple trichomes beneath. .... 23. *A. humile*

i. Rhizome short- to long-creeping, with the scales spreading, the petiole bases usually well spaced; lamina usually 1-pinnate, segments glabrous or nearly so beneath. .... 10. *A. petiolatum*

h. Segments green, usually shining, beneath, the sterile ones or portions unevenly biserrate; rhizome short-creeping, with appressed scales, the petiole bases approximate. .... 11. *A. obliquum*

b. Lateral ultimate segments asymmetrical in their apical half, or in *A. latifolium* and *A. villosissimum*, if symmetrical, then the lamina bi-pinnate and the terminal pinna about the same size as the laterals and usually narrowed at the base; lamina bipinnate, at least above the basal pinnae, or 3- to 4-pinnate in *A. pectinatum*. .... j.

j. Rachis and pinna-rachises glabrous or puberulent or pubescent with simple trichomes. .... k.

k. Pinna-rachises puberulent or pubescent only on the upper side, glabrous below. .... 20. *A. tomentosum*

k. Pinna-rachises glabrous, or puberulent or pubescent on all sides. .... l.

l. Pinnules nearest the rachis definitely asymmetrical. .... m.

m. Pinnules spaced, acute, pinna-rachises puberulent. .... 15. *A. Kalbreyeri*

m. Pinnules closely imbricate, broadly obtuse, pinna-rachises glabrous. .... 21. *A. macrocladum*

l. Pinnules nearest the rachis, or at the base of the penultimate segments, nearly or quite symmetrical. .... n.

n. Lamina with a single rachis and a more or less distinct terminal pinna that is broadest at the base, with at least the upper lateral pinnae with their inner pinnule closely overlaying the rachis. .... o.

o. Pinna-rachises whitish pubescent. .. 26. *A. sessilifolium*

o. Pinna-rachises puberulent. .... 27. *A. Henslovianum*

n. Lamina with a divided rachis and no terminal pinna, or with a single rachis and a distinct terminal pinna that is somewhat reduced at the base and with the lateral pinnae with their inner pinnules hardly overlaying the rachis. .... 29. *A. patens*

j. Rachis and pinna-rachises scaly or rufous pubescent-scaly. .... p.

p. Segments bearing usually numerous (sometimes few) simple trichomes beneath, in no. 23, these sometimes mixed with scales. .... q.

q. Pinna-rachises scaly with long, freely ciliate scales, one to three (rarely four) long sori on the upper edge of the fertile segments, segments acute. .... 16. *A. villosissimum*

q. Pinna-rachises pubescent-scaly, the scales sparsely if at all ciliate, five to usually 8-10 sori on the upper edge of the fertile segments, segments glaucous, obtuse. .... r.

r. Pinnules dull green to faintly glaucous beneath, those nearest the terminal segment of the pinna reduced, less than half as long as the longest pinnule (rarely more), usually 8-10 sori on the upper edge of the pinnule. .... 22. *A. terminatum*

r. Pinnules glaucous beneath, those nearest the terminal segment of the pinna not much reduced, more than half as long as the longest pinnule, usually 5-6 sori on the upper edge of the pinnule. .... 23. *A. humile*

p. Segments glabrous beneath or bearing usually few, sometimes stellate, scales. .... s.

s. Lamina commonly 4- to 5-pinnate at the base, segments deeply incised-lobed. .... 25. *A. pectinatum*

s. Lamina bipinnate, segments entire to coarsely serrate. .... t.

t. Sterile segments or portions rather finely and evenly serrate, terminal segments of pinnae usually fertile, obtuse to acute, pinnules nearest the terminal segment of the pinna usually not greatly reduced, about half as long as the longest pinnule. .... u.

u. Pinnules mostly herbaceous, glaucous, the indusia-bearing margins flat, terminal pinna reduced at the base, sori usually on the lower as well as the upper edge of the pinnules. .... 12. *A. latifolium*

u. Pinnules coriaceous, not glaucous, the indusia-bearing margins revolute, terminal pinna not or hardly reduced at the base, lower edge of pinnules without sori. .... 12. *A. serratodentatum*

t. Sterile segments or portions coarsely and often unevenly serrate, terminal segments of pinnae usually sterile, acute to acuminate. .... v.

v. Fertile pinnules with about 10-15 small sori on shallow lobes, none on the lower edge, some pinnules with 1-2 sori on the inner edge. .... 24. *A. cayennense*

v. Fertile pinnules usually with fewer than 10 large, arcuate sori on the hardly incised margin, sometimes some on the lower edge, none on the inner edge. .... w.

w. Pinnules nearest the terminal segment of the pinna not greatly reduced, about half as long as the longest pinnule, segments green beneath, indusium-bearing margins flat. .... 14. *A. villosum*

w. Pinnules nearest the terminal segment of the pinna greatly reduced, less than half as long as the longest pinnules. .... x.

x. Several sori on the upper and outer edges of the fertile pinnules. .... y.

y. Rhizome long-creeping, the petiole bases distant, pinnules with sterile tips mostly turned toward the apex of the pinna and acute. .... 17. *A. tetraphyllum*

y. Rhizome usually short-creeping, often knotted, the petiole bases adjacent, pinnules with sterile tips mostly straight and obtuse. .... 18. *A. fructuosum*

x. One, rarely two, sori on the upper edge of the fertile pinnules, rarely another on the outer edge. .... 19. *A. pulverulentum*

a. Ultimate segments definitely, although sometimes shortly, stalked, or most of them so. .... z.

z. Rachis and other axes of the lamina glabrous, or in *A. Poiretii*, rarely with some ceraceous indument. .... aa.

aa. Segments not articulated, the stalk passing evenly into the basal veins, deciduous by irregular fracture of the stalk. ...... bb.

bb. Sori borne on both sides of the ovate-lanceolate, long-acute to acuminate segments. .... 4. *A. platyphyllum*

bb. Sori borne on the convex outer edge of the cuneate to flabellate-orbicular, rounded, segments. .... cc.

cc. Sterile margins of the segments with each vein ending in a tooth, segments cuneate, with a pronounced cartilaginous border. .... 30. *A. Capillus-Veneris*

cc. Sterile margins of the segments with each vein ending in a sinus between the definite or indefinite teeth. .... dd.

dd. Pinnae subsessile, the lower as well as the upper with the inner upper pinnules overlaying the rachis. .... ee.

ee. Inner upper pinnule of lower pinnae simple. .... 31. *A. subvolubile*

ee. Inner upper pinnule of lower pinnae divided into two ultimate segments. .... 32. *A. concinnum*

dd. Pinnae, or at least the basal or lower ones, definitely stalked, the inner upper pinnule on them not or hardly overlaying the rachis. .... ff.

ff. Fertile lamina (rarely bi-) 3- to 4-pinnate, triangular to ovate-lanceolate. .... gg.

gg. Many ultimate segments symmetrically or asymmetrically cuneate, sori orbicular to suborbicular. .... 33. *A. Raddianum*

gg. Many ultimate segments orbicular to suborbicular, sori oblong or lunate, or many so. .... 34. *A. Poiretii*

ff. Fertile lamina 1- to bipinnate, oblong to oblong-tapering, sori orbicular, usually closely spaced. .... 36. *A. Ruizianum*

aa. Segments articulated at the junction with the stalk, deciduous by a sharp, clean break, the apical portion of the stalk enlarged (in the mature lamina or portions of it). .... hh.

hh. Ultimate segments flabellate-orbicular to cuneate, sori borne on the convex outer edge. .... ii.

ii. Lamina bi- to tripinnate, sterile margins of the segments with each vein ending in a sinus between the usually definite teeth, rachis with segments to the apex, not rooting. .... 35. *A. Orbignyanum*

ii. Lamina 1-pinnate, sterile margins of the segments sharply serrate with each vein ending in a tooth, some leaves with a long, barren, usually rooting, rachis tip. .... 39. *A. deflectens*

hh. Ultimate segments trapeziform to ovate-acuminate, sori borne on the upper and outer edges. .... jj.

jj. Segments mostly trapeziform, bluntly acute or rounded. .... kk.

kk. Segments short-stalked, terminal segments of the pinnae acute to acuminate. .... 1. *A. Mathewsianum*

kk. Segments long-stalked, terminal segments of the pinnae bluntly acute. .... 2. *A. peruvianum*

jj. Segments mostly ovate-cuneate, occasionally with an acuminate auricle, concavely acuminate. .... 3. *A. anceps*

z. Rachis and other axes of the lamina minutely puberulent (on the upper side) or short-pubescent (rarely glabrate), segments often pubescent beneath. .... ll.

ll. Rachis and other axes of the lamina minutely puberulent only on the upper side, segments glabrous beneath. ...... 28. *A. lobatum*

ll. Rachis and other axes of the lamina short-pubescent all over, to rarely glabrate, segments pubescent beneath, to rarely glabrate. .... mm.

mm. Ultimate segments not or shallowly and closely cleft, lamina bipinnate at the base, 1-pinnate above, segments glabrous above, sori orbicular to suborbicular. .. 37. *A. imbricatum*

mm. Ultimate segments deeply cleft into ca. 4-7 spreading lobes, lamina bi- to tripinnate, segments pubescent above as well as beneath, rarely they and the axes of the lamina glabrate, sterile margins of the segments with each vein ending in a tooth, sori straight or nearly so. .... 38. *A. digitatum*

1. **Adiantum Mathewsianum** Hook. Sp. Fil. 2: 35. 1851. Type: Chachapoyas, Peru, *Mathews 3296*, K! photo US, fragment *s.n.* ex K, NY! FIG. 96.

Rhizome not seen; leaves evidently large, perhaps to 1 m. or more, petiole glabrous, ebeneous or slightly glaucous, rachis similar; lamina probably broadly ovate-triangular, to quadripinnate, pinnae widely alternate, the basal very large, ultimate segments trapeziform, bluntly acute (the terminal one acute to acuminate) glabrous, short-stalked, articulate, the dark color of the stalk not entering the segment, of moderate size, ca. 2-2.5 cm. long, the inner edge often overlying the axis; sori commonly borne on all but the basal edge, many, roundish to short-oblong or lunate.

A glabrous species with trapeziform and blunt segments. The segment stalks are definite although rather short. In the shape of the segments and length of their stalks it differs from the related *A. trapeziforme* which has longer and slender segment-stalks and the segments themselves are concavely acute or acuminate. This latter species was erroneously reported from Peru by Hieronymus (Hedwigia 48: 237. 1909) on the basis of *Stübel 1084.*

Peru to Paraguay.

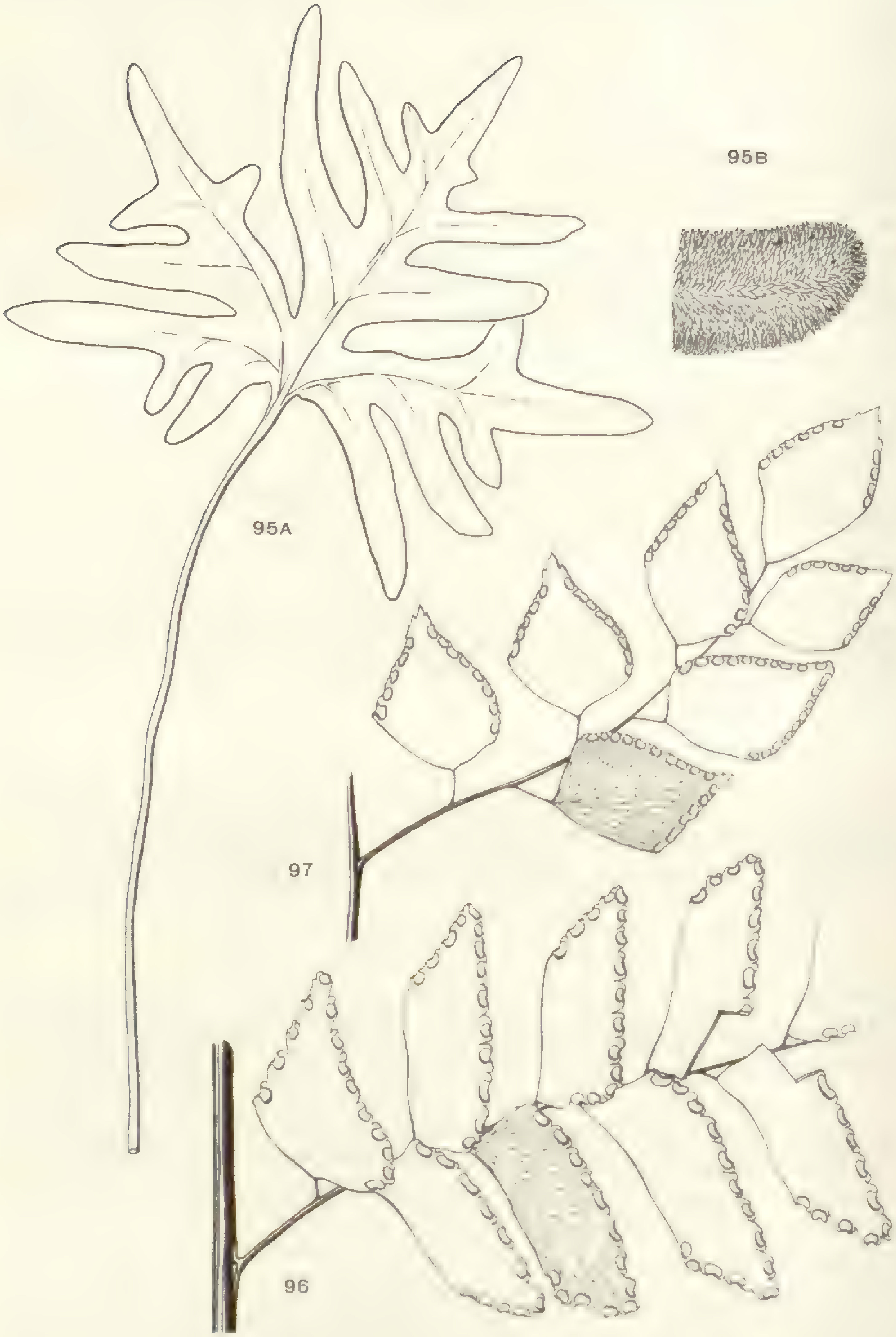
Amazonas to Junín, 1200 m.

Specimens seen: AMAZONAS: Chachapoyas, *Mathews* (NY), *3296* (K). SAN MARTIN: Tabalosos, *Stübel 1084* (B). JUNIN: La Merced, Chanchamayo, *Soukup 1116* (F); Chanchamayo, 1918, *Esposto* (USM).

2. **Adiantum peruvianum** Kl. Linnaea 18: 555. 1845. Syntypes: Vitoc, Peru, *Ruiz 25*, B! Chachavani, *Ruiz 27*, B! fragments ex B, US! FIG. 97, MAP 27.

Rhizome large and massive, very short-creeping; leaves to 1 m. tall, petiole ebeneous, glabrous, shining or slightly glaucous, rachis the same; lamina broadly ovate-triangular, to tripinnate (small ones elongate-triangular or oblong, once to bipinnate), pinnae widely alternate, the basal largest, ultimate segments ovate-trapeziform, bluntly acute or rounded (the terminal bluntly acute), glabrous, long-stalked, articulate, the dark color of the stalk not entering the segment, large, commonly ca. 5 cm. long; sori borne on the upper and outer edges, few if any on the inner edge, many, roundish to short-oblong or lunate.

The bluntly acute segments distinguish this species from the related *A. anceps* and *A. platyphyllum*. The long segment stalks and the larger segments distinguish it from the previous species *A. Mathewsianum*. The fertile leaves may be 1-pinnate, or in larger specimens bi- or tripinnate.



FIGS. 95-97. Fig. 95. *Saffordia induta:* A, leaf, × ½, Peru, *Sagastegui 2938*, GH; B, segment, lower surface, × 1½, *idem.* Fig. 96. *Adiantum Mathewsianum:* base of fertile pinna, × 1, Peru, *Soukup 1116*, F. Fig. 97. *A. peruvianum:* fertile pinna, × ½, Peru, *Soukup 2185*, US.

Ecuador to Bolivia.

In rich humus in deep woods or on canyon sides, Loreto to Cuzco, 750-2800 m.

Selected specimens: LORETO: Boquerón del Padre Abad, Aug. 10, 1943, *Ridoutt* (USM). HUANUCO: Cayumba, *Ferreyra 1873* (GH, USM); Puente Durand, north of Huánuco, valley of Río Chinchao, *Stork & Horton 9448* (F, GH, UC); gorge of Río Chinchao, *Tryon & Tryon 5313* (BM, F, MO, U, US, USM); Tingo María, *Tryon & Tryon 5236* (BM, F, MO, U, USM). JUNIN: La Merced, *Soukup 1115* (F), *2568* (US); Puente San Felix, *Cerrate 2869* (GH, USM); 10 km. sw. of San Ramón, *Tryon & Tryon 5450* (BM, F, MO, USM). CUZCO: Santa Rosa, Urubamba valley, *Cook & Gilbert 1714* (US); Quillabamba, *Bües 1236* (US).

3. **Adiantum anceps** Maxon & Morton, Amer. Fern Jour. 24: 15. 1934. Type: La Merced, Junín, Peru, *Killip & Smith 24069*, US!; isotype: NY! FIG. 98, MAP 28.

Adiantum Crespianum Bosco, Nuovo Giorn. Bot. Ital. n.s. 45: 148, t.x, fig. 2. 1938. Type: Indanza, Ecuador, *C. Crespi;* isotype: US!

Rhizome large and massive, short- or very short-creeping; leaves to 1 m. tall, petiole ebeneous, glabrous, shining or slightly glaucous, rachis the same; lamina broadly ovate-triangular, to tripinnate (small ones elongate-triangular or oblong, 1- or bipinnate), pinnae widely alternate, the basal largest, ultimate segments ovate-cuneate, concavely acuminate, glabrous, long-stalked, articulate, the dark color of the stalk not entering the segment, large, commonly ca. 6 cm. long; sori borne on the upper and outer edges (the inner and lower not well defined), numerous, roundish to mostly short-oblong to oblong or lunate.

This species is rather closely related to *A. peruvianum* from which it was segregated. It differs especially in the concavely acuminate rather than bluntly acute segments. A number of specimens have some segments with an acuminate auricle. The related *A. subcordatum* of Brazil and British Guiana has the rhizome creeping and stout with the petiole bases spaced, the scales are secund, falcate, rigid and entire, the petiole and rachis are reddish-brown and the segments are glaucous beneath, and acute to acuminate with straight sides. *Adiantum anceps*, on the other hand, has a massive rhizome with the petiole bases adjacent; the scales are toothed or ciliate, not rigid and more or less straight; the petiole and rachis are atropurpureous to nearly black; and the segments are dull to green beneath and concavely acuminate.

Ecuador and Peru.

In forests, San Martín to Cuzco, 230-1500 m.

Selected specimens: SAN MARTIN: Lamas, *L. Williams 6445* (F, GH, NY, US); Juan Jui, Alto Río Huallaga, *Klug 4255* (BM, F, GH, MO, NY, UC, US, USM); Pongo de Cainarachi, Río Cainarachi, *Klug 2688* (BM, F, GH, MO, NY, US). HUANUCO: Tingo María, *Tryon & Tryon 5288* (BM, F, GH, MO, NY, U, UC, US, USM). JUNIN: Monte Rico, La Merced, *Soukup 3507* (GH, MO, UC); La Merced, *Killip & Smith 23478* (F, GH, NY, US), *Cerrate 2848* (GH, USM). CUZCO: Quellouno, prov. Convención, *Vargas 13556* (GH).

4. **Adiantum platyphyllum** Sw. Svenska Vet. Akad. Handl. 1817: 74, t. 3, fig. 6. 1817. Type: Villa Rica, Minas Geraes, Brazil, *Freyreis* (Herb. Sw.) S-PA! fragment US! FIG. 99.

Rhizome moderately stout, short-creeping, the petiole bases crowded; leaves up to ca. 0.7 m. tall, petiole ebeneous or nearly so, glabrous, shining or somewhat glaucous, rachis the same; lamina broadly triangular to ovate-triangular, bipinnate (small ones oblong, 1-pinnate), pinnae widely alternate, the basal largest, ultimate segments ovate-lanceolate, cuneate, long-acute to long-acuminate, glabrous, decidedly glaucous beneath, long-stalked, not articulate, the dark color of the stalk entering the base of the segment beneath, large, commonly 5-10 cm. long; sori borne on the upper and outer edges (the inner and lower not well defined), numerous, oblong to long-oblong or long-lunate.

The long-stalked, glaucous and long-acuminate segments combine to make this a distinctive species. It is easily separated from any of the preceding three species by the character of the segment-stalk. In *A. platyphyllum* the dark color enters the base of the segment; in the other species the stalk is articulated at its apex and the dark color abruptly ends there.

Ecuador to Bolivia and Brazil.

In forests, San Martín to Junín, 700, to usually ca. 1000, to 1700 m.

Selected specimens: SAN MARTIN: San Roque, *L. Williams 7446* (F, US); Zepelacio, near Moyobamba, *Klug 3490* (F, GH, MO, NY, US). HUANUCO: Pozuzo, *Macbride 4570* (F, US). JUNIN: Chanchamayo valley, *Schunke 4* (F, US), *100* (US), *152* (F), *445*, *1366*, *1368* (F, US), *1445* (F).

5. **Adiantum macrophyllum** Sw. Nov. Gen. Sp. Prod. 135. 1788. Type: Jamaica, *Swartz*, (Herb. Sw.), S-PA! FIG. 100, MAP 29.

Rhizome moderately stout, short to moderately creeping; leaves mostly 30-60 cm. tall, petiole ebeneous or atropurpureous, glabrous, shining or slightly glaucous, rachis the same; lamina oblong-acute or

Maps 27-30. Map 27, *Adiantum peruvianum.* Map 28, *A. anceps.* Map 29, *A. macrophyllum.* Map 30, *A. obliquum.*

elongate-triangular, 1-pinnate, pinnae essentially opposite (rarely some alternate), entire, long-triangular, to ovate-triangular, broadly cuneate, occasionally auriculate or biauriculate, acute to acuminate, glabrous, glaucous or dull beneath, subsessile, not articulate, the dark color of the short stalk entering the base of the pinna, large, commonly 6-9 cm. long; one long sorus on each side of the pinna, rarely two or three on some pinnae.

Several characters combine to make this one of the most distinctive species in the genus. The lamina is 1-pinnate with opposite (rarely sub-opposite), glabrous, glaucous and broad pinnae. Typically there is a single long sorus on each side of the pinna.

Guianas to Colombia to Bolivia and Brazil; Mexico; West Indies.

It grows in woods, in dense forests, on shady banks and in rocky places with soil, San Martín and Loreto to Madre de Dios and Puno, 200-2500 m.

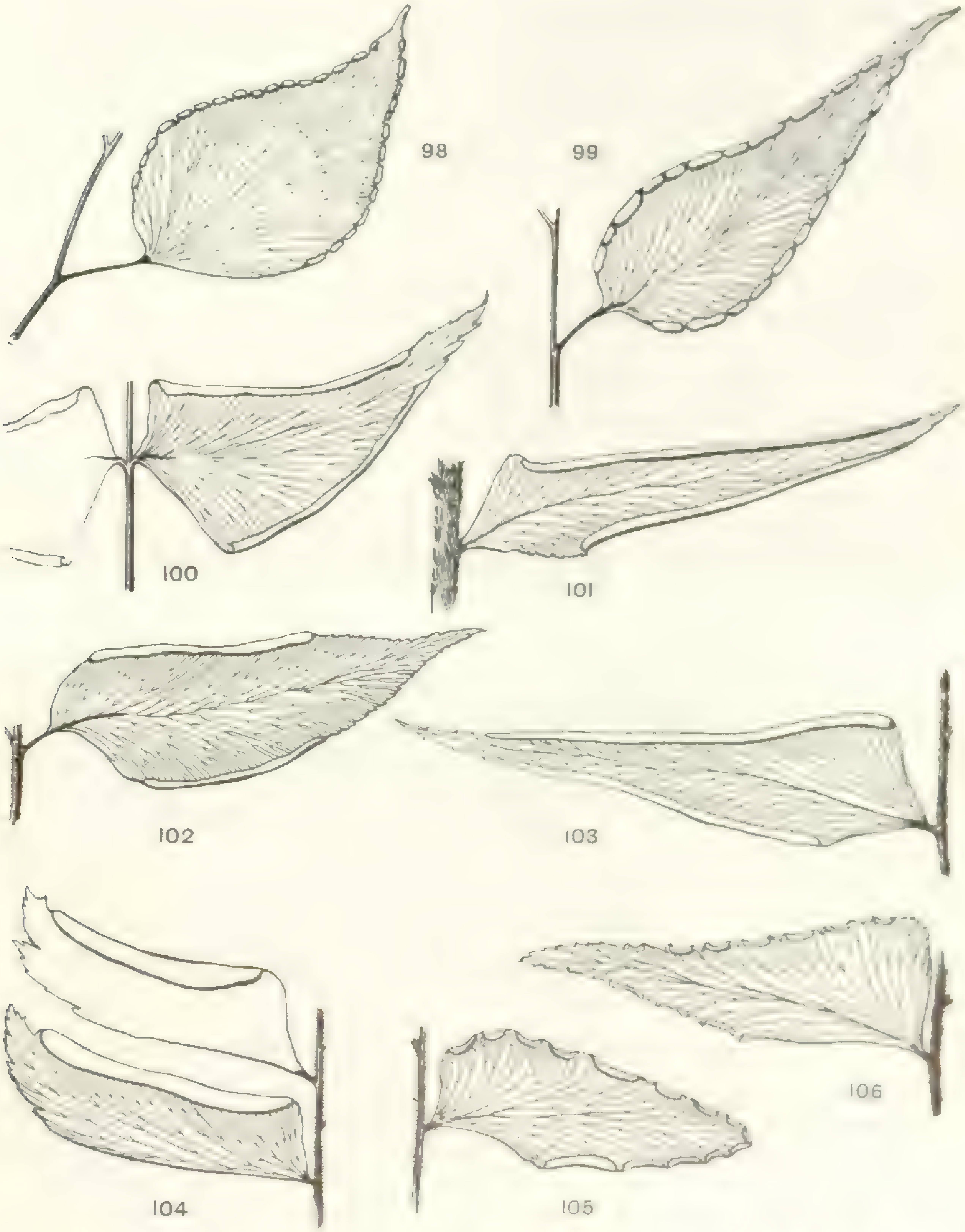
Selected specimens: SAN MARTIN: Tarapoto, *Woytowski 35247* (MO, UC): San Roque, *L. Williams 7447* (F). LORETO: Río Marañon, above Pongo de Manseriche, *Mexia 6179a* (UC). HUANUCO: Hacienda Mercedes, Exito to Mercedes, *Mexia 8186* (F, GH, MO, UC, US); Río Bella, Tingo María, *Soukup* (US), *3090* (F, MO); Tingo María, *Ferreyra 10308* (GH, USM). JUNIN: Pichis trail, between San Nicolás and Azupizú, *Killip & Smith 26112* (F, NY, US); La Merced, *Soukup 1111* (F). AYACUCHO: Estrella, between Huanta and Río Apurímac, *Killip & Smith 23056* (F, GH, NY, US). CUZCO: Potrero, *Vargas 1704* (GH, MO), *8225* (MO, UC), *Tryon & Tryon 5388* (BM, F, MO, U, US, USM). MADRE DE DIOS: Alto Madre de Dios, *Rauh P1667* (B). PUNO: Chunchosmayo, prov. Sandia, *Weberbauer 1267* (B).

6. **Adiantum scalare** Tryon, Amer. Fern Jour. 47: 141, t. xv. 1957. Type: Río Santiago, Loreto, Peru, *Mexia 6162*, UC!; isotypes: BM! GH! K! MO! PH! FIG. 101.

Rhizome moderately stout, short-creeping, scales dull; leaves ca. 60-75 cm. tall, petiole ebeneous, deciduously scaly, rachis similar but persistently scaly; lamina ovate or oblong-ovate, 1-pinnate, pinnae closely alternate, mostly 8-13 cm. long, more or less long-triangular, entire, often auriculate, with long brown trichomes beneath; one very long sorus on each side of the pinna.

This distinctive species is 1-pinnate and has the rachis scaly and the under surface of the pinnae pubescent. Other 1-pinnate species, or those occasionally 1-pinnate, have the rachis glabrous or pubescent-scaly and the segments glabrous. The long, narrowly triangular pinnae usually have a small auricle on the upper edge at the base and sometimes a smaller one on the lower edge near the base.

Endemic to Peru.



FIGS. 98-106. Fig. 98. *Adiantum anceps:* fertile ultimate segment, × ½, Peru, *Klug 2688*, MO. Fig. 99. *A. platyphyllum:* fertile ultimate segment, × ½, Peru, *Schunke 152*, F. Fig. 100. *A. macrophyllum:* fertile pinna, × ½, Peru, *Killip & Smith* [illegible], GH. Fig. 101. *A. scalare:* fertile central pinna, × ½, Peru, *Mexia* [illegible], UC. Fig. 102. *A. Poeppigianum:* fertile pinna, × ½, Peru, *Killip & Smith* [illegible], US. Fig. 103. *A. lucidum:* fertile pinna, × ¾, Trinidad, *Broadway* [illegible], MO. Fig. 104. *A.* [illegible]: fertile pinnae, × 1, Ecuador, *Barclay*, US. Fig. 105. *A. petiolatum:* fertile pinna, × 1, Peru, *Schunke 377*, GH. Fig. 106. *A. obliquum:* fertile pinna, × 1, British Guiana, *A. C. Smith 2432*, GH.

In dense forest, Amazonas and Junín, at 200 to 340 m.

Specimens seen: AMAZONAS: Mouth of Río Santiago, *Tessmann 4276* (B, NY); Río Santiago, *Mexia 6162* (GH, MO, PH, UC). JUNIN: Cahuapanas on Río Pichis, *Killip & Smith 26741* (F, GH, NY).

7. **Adiantum Poeppigianum** (Kuhn) Hieron. Hedwigia 48: 231. 1909. FIG. 102.

Adiantum lucidum var. *Poeppigianum* Kuhn, Jahrb. Bot. Gart. Berlin, 1: 340. 1881. Type: Prov. Maynas, (Loreto), Peru, *Poeppig 2268*, B!; isotypes: BM! GH! LE! US!

Rhizome rather slender, long-creeping, the petiole bases spaced, scales dull; leaves ca. 30-50 cm. tall, petiole ebeneous, deciduously pubescent-scaly, rachis similar; lamina roundish-ovate to ovate-oblong, usually 1-pinnate, sometimes sparingly bipinnate, entire pinnae lanceolate-cuneate to ovate-lanceolate and subcordate, mostly 6-11 cm. long, subopposite to alternate, glabrous or slightly scaly beneath, not articulate, the dark color of the stalk entering the base of the pinna, midvein distinct to the apex; a single very long sorus on each side of the pinna or pinnule.

This species is somewhat variable in the shape of the pinnae. Usually the sterile ones are about twice as broad as the fertile, although occasionally the latter may also be broad. The base of the pinna varies from cuneate to nearly cordate. It is separated from the allied *A. lucidum* by the distinct midvein of the pinna, which is dark colored at the base. The related *A. phyllitidis* has a long dark colored portion of the midvein and the sterile margins of the pinnae are slightly and remotely crenate-serrate while *A. Poeppigianum* has a short dark colored portion of the midvein and sterile margins are minutely and densely serrate.

Endemic to Peru.

In dense forest, Amazonas to Junín, 135-500 m.

Selected specimens: AMAZONAS: entre Aramango y Montenegro, prov. Bagua, *López et al. 4227* (GH). SAN MARTIN: Tarapoto, *L. Williams 6141* (F, US); upper Río Huallaga, *L. Williams 6190* (F, US); Juan Jui, *Ferreyra 4525* (GH, USM). LORETO: Puerto Arturo, lower Río Huallaga below Yurimaguas, *Killip & Smith 27724* (F, NY, US); Santa Rosa, below Yurimaguas, *Killip & Smith 28995* (NY, US); Yurimaguas, *Killip & Smith 28013* (F, NY, US); lower Río Huallaga, *L. Williams 5097* (F, US). JUNIN: Satipo, Aug. 1940, *Ridoutt* (GH, USM).

8. **Adiantum lucidum** (Cav.) Sw. Syn. Fil. 121. 1806. FIG. 103.

Pteris lucida Cav. Descr. 266. 1802. Type: Guaranda, Ecuador, *Née*; isotype: S-PA!

Rhizome moderately stout, short-creeping, scales dull; leaves mostly 30-60 cm. tall, petiole ebeneous to dark brown, deciduously pubescent-scaly, rachis similar; lamina oblong, 1-pinnate, or ovate-triangular, bipinnate, entire pinnae and the pinnules asymmetrically ovate-lanceolate to long-triangular, unequally cuneate, ca. 4-10 cm. long, alternate, glabrous or slightly scaly beneath, not articulate, the dark color of the stalk entering the base of the pinna or pinnule, midvein indistinct or lacking in the apical half; a single long sorus on each side of the pinna or pinnule, or the latter with only one on the upper edge.

Guianas to Colombia and Panama, south to Peru; Trinidad and Tobago.
Forests, Junín.

Specimens seen: JUNIN: Río Satipo, 1940, *Ridoutt* (US, USM); Pichita Caluga, Chanchamayo, *Walden 64* (BM).

9. **Adiantum alarconianum** Gaud. Voy. Bonit. Bot. t. 99. 1846. Type: Guayaquil, Ecuador, April, 1836, *Gaudichaud*, P! fragment US! isotype: B! FIG. 104.

Adiantum incisum Pr. Rel. Haenk. 1: 61, t. 10. f. 3. 1825, not Forsk. 1775. Syntypes: Guayaquil, Ecuador, *Haenke*, *9* (var. *α*), *10* (var. *β*); isotypes: BM! W!

Rhizome moderately stout, short-creeping, scales iridescent; leaves ca. 30-50 cm. tall, petiole reddish-brown to dark brown, glabrous or slightly pubescent-scaly on the upper side, rachis similar but definitely pubescent-scaly on the upper side, glabrous elsewhere; lamina linear to broadly linear and 1-pinnate or broadly ovate-oblong and bipinnate, entire pinnae or pinnules oblong-falcate to long-triangular, strongly asymmetrical at the base, ca. 1-4 cm. long, alternate, glabrate beneath, sessile or subsessile; a single long sorus borne on the upper edge.

The iridescent rhizome scales and the indument confined to the upper surface of the rachis characterize this species. The sterile pinnae are deeply incised and the fertile usually have a single long sorus on the upper edge. In bi-pinnate blades only the basal or lower pinnae are 1-pinnate.

Ecuador and adjacent Peru.
Woods, Tumbes, 650 m.

Specimens seen: TUMBES: between Cancho and Cotrina, *Coronado 218* (GH, UC); Tumbes to Cancho, *Coronado 228* (UC).

10. **Adiantum petiolatum** Desv. Ges. Naturfr. Freunde Berl. Mag. 5: 326. 1811. Type: uncertain, not seen at P. FIG. 105.

Adiantum Kaulfussii Kze. Linnaea 21: 221. 1848. Lectotype: *Sieber, Fl. Martin. 371;* isotype: B!

Rhizome slender, long-creeping, with spreading scales, the petiole bases usually well spaced; leaves ca. 20-40 cm. long, petiole ebeneous or atropurpureous, glabrate, rachis often somewhat lighter; lamina more or less oblong and 1-pinnate or deltoid and bipinnate, with the pinnate pinnae few, entire pinnae ovate-lanceolate to oblong, strongly asymmetrical at the base, ca. 3-5 cm. long, pinnae and pinnules dull, usually glaucous beneath, sterile margins evenly serrate; sori several, oblong-arcuate to long-arcuate or nearly straight, more numerous on the upper than on the outer edge.

This is a rather critical species and somewhat variable; the rachis, for example, is rarely glabrate. The characters given in the key to separate it from *A. obliquum* and *A. humile* are quite satisfactory with adequate material at hand but with partial specimens identification is more difficult. It is apparently also closely related to *A. latifolium*. In that species the terminal pinna is conform with the several lateral ones and it is usually reduced at the base; its segments are sessile or subsessile. In *A. petiolatum* the terminal pinna in bipinnate laminae is much larger than the few lateral ones and broadest at the base, its basal segments have definite stalks.

Guianas to Colombia, to Bolivia and Brazil; Mexico; West Indies.

In forests, Loreto, Junín and Cuzco, to 700 m.

Selected specimens: LORETO: near Iquitos, *Tryon & Tryon 5191* (BM, F, GH, MO, U, UC, US, USM); Salinas, Río Mazán, *Schunke 377* (F, GH, NY, UC, US, USM); Río Santiago above Pongo de Manseriche, *Mexia 6235* (BM, F, GH, MO, PH, US). JUNIN: Río Satipo, Aug. 1940, *Ridoutt* (USM). CUZCO: Atalaya, prov. Paucartambo, *Vargas 13301* (GH).

11. **Adiantum obliquum** Willd. Sp. Pl. 5: 429. 1810. Syntypes: Caracas, Venezuela, *Bredemeyer* (Herb. Willd. 20067-1) B! photo BM, GH; Porto Rico, *Ventenat* (Herb. Willd. 20067-2) B! photo BM, GH. FIG. 106, MAP 30.

Rhizome slender, long-creeping but with usually closely spaced petiole bases, often branched, with appressed scales; leaves ca. 20-60 cm. long, petiole atropurpureous to dark reddish-brown, deciduously or persistently pubescent-scaly, rachis similar, usually lighter; lamina broadly linear to elongate-triangular and 1-pinnate or deltoid to deltoid-ovate and bipinnate, with the pinnate pinnae few, entire pinnae and pinnules oblong to long-triangular, strongly asymmetrical at the base, ca. 2-6 cm. long, green, usually shining beneath, sterile margins unevenly biserrate; sori several, short to long-oblong, straight or arcuate, more numerous on the upper than on the outer edge.

This species is closely allied to the previous, *A. petiolatum*. Adequate material may be satisfactorily determined by the characters in the key. Bipinnate leaves may be confused with a number of the strictly bipinnate species. However, in *A. obliquum* as in *A. petiolatum*, the terminal pinna of a bipinnate lamina is larger than the few laterials, broadest at the base and its basal segments are usually stalked.

Guianas to Colombia to Bolivia and Brazil; Mexico; West Indies.

It grows in dense forests or on wooded slopes, San Martín and Loreto to Junín, 350-1500 m.

Selected specimens: SAN MARTIN: Across the Huallaga on trail to Monson (Tingo María), *Allard 21853* (US). LORETO: Balsapuerto, lower Río Huallaga basin, *Killip & Smith 28508* (F, NY, US); near mouth of Río Santiago, above Pongo de Manseriche, *Mexia 6206a* (GH, UC, US); Río Itaya, near Iquitos, *Tryon & Tryon 5201* (BM, F, MO, U, US, USM). HUANUCO: Tingo María, *Tryon & Tryon 5253* (BM, F, MO, U, US, USM), *5293* (BM, F, USM), *Ferreyra 10259* (USM). JUNIN: Chanchamayo valley, *Schunke 95* (F), *763* (US), *831* (F).

12. **Adiantum latifolium** Lam. Encycl. 1: 43. 1783. Type: uncertain, there is no specimen in Herb. Lamarck; Brazil, *Commerson* (Herb. Jussieu no. 1408) P! photo GH, US may serve to fix the application of the name. **FIG. 107, MAP 31.**

Rhizome slender, very long-creeping; leaves ca. 30-70 cm. tall, petiole brown to atropurpureous, deciduously pubescent-scaly, the rachis persistently so; lamina deltoid to ovate-deltoid or ovate-oblong, bipinnate, pinnae ca. 10-15 cm. long, pinna-rachises pubescent-scaly, the terminal pinna reduced at the base, pinnules herbaceous, glaucous beneath, glabrate, with the sterile ones evenly serrate, those nearest the usually acute terminal segment of the pinna usually not much reduced; sori several, oblong, usually on the lower as well as the upper edge.

This species is distinguished from the other bipinnate species by its long-creeping rhizome with the petioles borne at intervals, its glaucous segments, the sterile ones with the margins finely and evenly serrate, and the usually distinct midvein of the pinnules.

Tropical America.

In woods and dense forest, Loreto to Cuzco and Madre de Dios, 100-1000 m.

Selected specimens: LORETO: Río Putumayo, Peru-Colombia boundary, *Klug 1631* (F, GH, MO, NY, US); Iquitos, *Killip & Smith 27236* (F, GH, NY, US); Fundo Indiana, dist. Iquitos, *Mexia 6389* (BM, F, GH, MO, NY, PH, UC, US); Río Itaya, near Iquitos, *Tryon & Tryon 5170* (BM, F, MO, U, US, USM). JUNIN: east of Quimiri Bridge, near La Merced, *Killip & Smith 24003* (NY, US). AYACUCHO: Río Apurímac valley, near Kimpitiriki, *Killip & Smith 22925* (GH, NY, US). CUZCO: Hacienda Kosñipata, Socorro, prov. Paucartambo, *Vargas 10202* (MO, UC). MADRE DE DIOS: Maldonado, *Rauh P722* (B).

13. **Adiantum serratodentatum** Willd. Sp. Pl. 5: 445. 1810. Type: Caripe, Venezuela, *Humboldt & Bonpland* (Herb. Willd. 20088, the two sterile leaves) B! photo BM, GH. FIG. 108.

Rhizome slender, very long-creeping; leaves ca. 35-65 cm. tall, petiole brownish to atropurpureous, deciduously pubescent-scaly, the rachis persistently so; lamina deltoid-ovate to oblong-ovate, bipinnate, pinnae ca. 6-11 cm. long, pinna-rachises pubescent-scaly, the terminal pinna not or hardly reduced at the base, pinnules coriaceous, not glaucous, glabrate or slightly scaly beneath, sterile ones evenly serrate, those nearest the usually obtuse terminal segment of the pinna not much reduced; sori few to several, roundish to oblong or sublunate, borne on the upper and outer, rarely the inner, edges.

This species is characterized by its coriaceous, usually small, oblong pinnules and the terminal pinna which is little, if at all, reduced at the base. The pinnules are commonly fertile except for the entire inner and lower edges; the other margins, when sterile, are usually finely and evenly serrate. The rhizome is cord-like and long-creeping as in the allied *A. latifolium*.

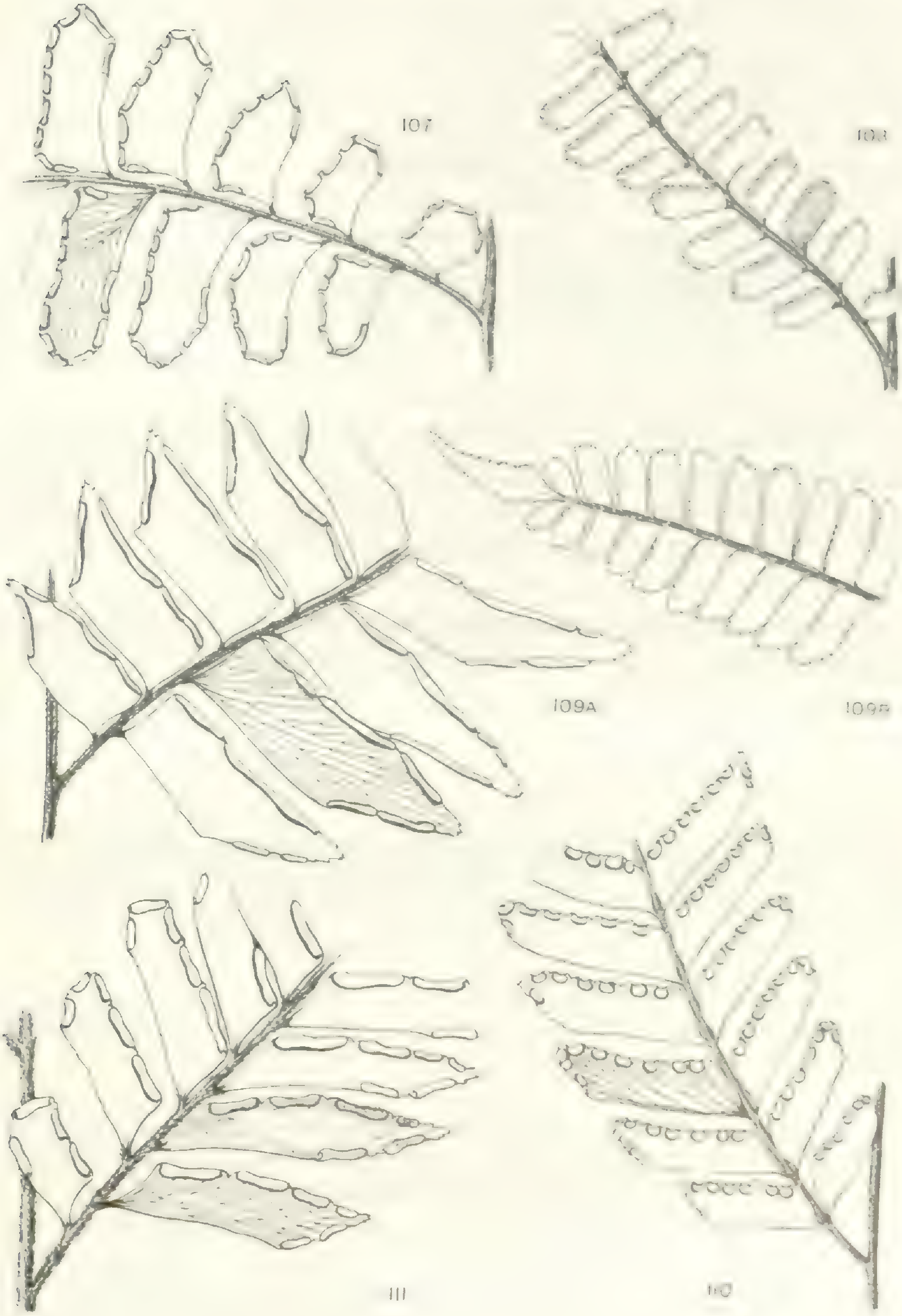
Guianas to Colombia, to Bolivia and Brazil; to Mexico; West Indies.

It grows in forests and in open habitats among grasses, San Martín and Piura, 750-1500 m.

Selected specimens: PIURA: Cerro de Chiriris, Pajonal, *Bües 1711* (US). SAN MARTIN: Zepelacio, near Moyobamba, *Klug 3462* (F, GH, MO, NY, US); Tarapoto, *Woytkowski 35103* (MO, UC), *L. Williams 5896* (F).

14. **Adiantum villosum** L. Syst. Nat. ed. 10, 2: 1328. 1759. Type: LINN 1252.10, photo A, is evidently this species. FIG. 109.

Rhizome moderately slender, rather short-creeping; leaves ca. 40-70 cm. tall, petiole dark reddish-brown to atropurpureous, deciduously pubescent-scaly, the rachis persistently so; lamina ovate-deltoid to ovate-oblong, bipinnate, pinnae ca. 10-20 cm. long, pinna-rachises pubescent-scaly, the terminal pinna reduced at the base, pinnules glabrate or slightly scaly beneath, sterile ones coarsely and unevenly serrate, those nearest the acute to acuminate terminal segment not much reduced; sori few to several, oblong to linear, borne on the upper and outer edges.



FIGS. 107-111. Fig. 107. *Adiantum latifolium:* base of fertile pinna, × 1, Peru, *Mexia 6389*, MO. Fig. 108. *A. serratodentatum:* base of fertile pinna, × 1, Peru, *Klug 3462*, MO. Fig. 109. *A. villosum:* A, base of fertile pinna, × 1, Colombia, *H. H. Smith 947*, GH; B, apex of sterile pinna, × ½, *idem.* Fig. 110. *A. Kalbreyeri:* base of fertile pinna, × 1, Peru, *Mexia 8175*, GH. Fig. 111. *A. villosissimum:* base of fertile pinna, × 1, Peru, *Macbride 5648*, F.

The pinnules near the apex of a pinna are about half as long as the longest on the pinna, rather than much smaller, and this difference distinguishes *A. villosum* from related species that also have coarse and irregular serrations on the sterile margins. In general aspect the leaves are otherwise very similar to those of *A. tetraphyllum.*

I have not been able to account satisfactorily for *Adiantum Ceciliae* Alston (Lilloa 30: 109, t. 4, 5. 1960, Type: moist sandstone on edge of forest, South bank of Río Perené, within 15 miles of confluence of Río Chanchamayo and Río Paucartambo, Junín, Peru, *Gascoyne-Cecil 50* BM!; paratype: *47*, BM!). The species seems to be close to *A. villosum* in the characters of the dimidiate, subtrapeziform pinnules, the short-creeping rhizome, the shape of the sori and the type of indument (or lack of it) on various parts of the leaf. All of these characters are within the range of variation of *A. villosum*, although they are not correlated as in *A. Ceciliae.* The pinnules have longer stalks than any I have seen in *A. villosum.*

Venezuela to Colombia, to Peru and Brazil; Mexico; West Indies.

Forests, Loreto, Junín and Cuzco, 700-1500 m.

Specimens seen: LORETO: Río Itaya, near Iquitos, *Tryon & Tryon 5197* (BM, F, GH, MO, USM). JUNIN: Chanchamayo valley, *Schunke 763* (F); La Merced, *Killip & Smith 23445* (NY, US), *Soukup 1110* (F). CUZCO: Quelloune, prov. Convención, *Vargas 13359* (GH).

15. **Adiantum Kalbreyeri** C. Chr. Ind. Fil. 28. 1905, based on *A. pilosum* Bak., Ann. Bot. 5: 207. 1891, not Fée, 1852. Type: Colombia, *Kalbreyer 956*, K! photo GH. FIG. 110.

Rhizome moderately stout, moderately long-creeping; leaves ca. 60-90 cm. tall, petiole ebeneous, dull or glaucous, deciduously puberulent, the rachis persistently so; lamina ovate, bipinnate, pinnae few, ca. 15-20 cm. long, pinna-rachises puberulent, the terminal pinna reduced at the base, pinnules glabrate, sterile ones coarsely and unevenly serrate, those nearest the long-acuminate terminal segment greatly reduced; sori several to numerous, roundish, borne on the upper and outer edges.

Costa Rica to Peru.

Forested slope, Huánuco, 1200 m.

Specimens seen: HUANUCO: Hacienda Mercedes, Balsa-Playa, dist. Churubamba, prov. Huánuco, *Mexia 8175* (BM, F, GH, MO, US).

16. **Adiantum villosissimum** Kuhn, Linnaea 36: 73. 1869. Type: Turbo, Panama, *Schott 65*, MO! fragments ex Engelm. B! FIG. 111.

Rhizome moderately slender, long-creeping; leaves ca. 50-80 cm. tall, petiole dark reddish-brown to atropurpureous, glaucous, persistently or deciduously scaly, the rachis scaly; lamina ovate to deltoid-ovate, bipinnate (sometimes the basal pinnae with a single branch on the lower side and then tripinnate), pinnae ca. 15-20 cm. long, pinna-rachises scaly, the terminal pinna reduced at the base, pinnules with numerous simple trichomes beneath, sterile ones unevenly serrate, those nearest the long-acuminate terminal segment greatly reduced; sori few, oblong to linear, sometimes arcuate, borne on the upper and outer edges.

The bipinnate lamina with the rachis and pinna-rachises scaly with freely ciliate scales and the segments with trichomes on the under surface combine to make this a very distinctive species. Related species with scales on the rachis have narrow scales and trichomes as well. Some leaves are tripinnate, the inner lower pinnule of the basal pinnae being well developed and fully pinnate.

Panama and Peru.

Dense forest and forested slopes, San Martín to Junín, 1100-1500 m.

Selected specimens: SAN MARTIN: Tarapoto, *Spruce 4665* (K). HUANUCO: Balsa Playa, prov. Huánuco, *Vargas 5317* (UC; USM, *s.n.*). Tingo María, *Aguilar 314* (USM). JUNIN: La Merced, Chanchamayo, *Soukup 1078* (F); Chanchamayo valley, *Schunke 105* (F), *872* (F); Schunke Hacienda, La Merced, *Macbride 5648* (F, US), *Killip & Smith 24691* (F, NY, US).

17. **Adiantum tetraphyllum** Willd. Sp. Pl. 5: 441. 1810. Syntypes: Herb. Willd. 20082-1, ex Vahl, and -2, Caripe, *Humboldt & Bonpland*, B! photos GH. FIG. 112.

Rhizome rather slender, long-creeping, the petiole bases distant; leaves ca. 50-90 cm. tall, petiole dark reddish-brown to atropurpureous, more or less deciduously pubescent-scaly as is the rachis; lamina broadly ovate to deltoid-ovate, bipinnate, pinnae ca. 10-18 cm. long, pinna-rachises pubescent-scaly, the terminal pinna reduced at the base, pinnules glabrate or slightly scaly beneath, the usually acute sterile tips turned toward the apex of the pinna, sterile ones unevenly serrate, those nearest the long-acuminate terminal segment greatly reduced; sori few to several, short-oblong to lunate, borne on the upper and also often on the outer edge.

The two species here recognized in the alliance of *A. tetraphyllum*, the true *A. tetraphyllum* and *A. fructuosum*, are maintained with some hesitation. The characters seem adequate but until the whole complex is worked out in the American tropics, their status will remain doubtful. The rhizome is long-creeping and the sterile apex of the pinnules is acute and mostly turned upward in *A. tetraphyllum*, while in *A. fructuosum* the rhizome is short-creeping, often massive with crowded petiole bases, and the sterile apex of the pinnules is obtuse and rather straight. In either species identification may be difficult in cases where the rhizome is lacking on a specimen or in some heavily fertile leaves that have few pinnules with a sterile apex.

Tropical America.

Dense forest and wooded slopes, Loreto, Huánuco south to Ayacucho and Madre de Dios, 100-1000 m.

Selected specimens: LORETO: Soledad on Río Itaya, *Killip & Smith 29573* (F); lower Río Huallaga, *L. Williams 5053* (NY). HUANUCO: Pampayacu, mouth of Río Chinchao, *Macbride 5029* (F). JUNIN: Chanchamayo valley, *Schunke 9* (F, US). La Merced, *Tryon & Tryon 5438* (BM, F, GH, MO, U, UC, US, USM). AYACUCHO: between Huanta and Río Apurímac, *Killip & Smith 22623* (F, NY, US), *22714* (NY, US). MADRE DE DIOS: Maldonado, *Rauh P749* (B).

18. **Adiantum fructuosum** Spreng. Syst. Veget. 4: 113. 1827. Type: Cuba, 1822, *Poeppig;* isotype: B! US! L, photo GH, US. FIG. 113.

Rhizome moderately stout to slender, rather short-creeping, the petiole bases commonly closely approximate; leaves ca. 60-100 cm. tall, petiole dark reddish-brown to atropurpureous, more or less persistently pubescent-scaly, sometimes densely so, the rachis similar; lamina broadly ovate, oblong-ovate or deltoid-ovate, bipinnate, pinnae ca. 10-20 cm. long, pinna-rachises pubescent-scaly, the terminal pinna reduced at the base, pinnules glabrate to moderately scaly beneath, the usually obtuse sterile tips usually straight, sterile ones unevenly and usually coarsely serrate, those nearest the long-acuminate terminal segment greatly reduced; sori few to several, roundish to usually short-oblong or lunate, borne on the upper and usually also on the outer edges.

The differences from *A. tetraphyllum* are discussed under that species.

Venezuela to Peru and Brazil; Mexico; West Indies.

Dense forest, Tumbes to Loreto, south to Cuzco, 135-1200 m.

Selected specimens: TUMBES: between Cancho and Cotrina, *Coronado 223* (GH, UC). AMAZONAS: ca. 40 km. s. of Bagua Grande, *Hutchison 1463* (GH). LORETO: Río Nanay, near Iquitos, *Tryon & Tryon 5177* (BM, F, GH, MO, U, US, USM); Yurimaguas, *Ferreyra 4990* (USM); La Victoria, on the Amazon, *L. Williams 2549* (F). HUANUCO: Pampayacu, *Kanehira 153* (GH, US); Tingo María, *Tryon & Tryon 5294* (BM, F, GH, MO, U, US, USM). CUZCO: Quellu-uno, *Bües 1702* (US).

19. **Adiantum pulverulentum** L. Sp. Pl. 2: 1096. 1753. Type: uncertain. FIG. 114.

Rhizome moderately stout, rather short-creeping; leaves ca. 30-90 cm. tall, petiole dark reddish-brown to ebeneous, more or less persistently pubescent-scaly, the rachis usually persistently so; lamina short-oblong to oblong-ovate, bipinnate, pinnae ca. 9-15 cm. long, pinna-rachises pubescent-scaly, the terminal pinnae reduced at the base, pinnules glabrate to somewhat scaly beneath, sterile ones coarsely serrate, those nearest the acute to long-acuminate terminal segment greatly reduced; one long sorus (rarely two) borne on the upper edge, rarely a shorter one also on the outer edge.

The single long sorus on the upper edge of the pinnules is sufficient to characterize this species. Occasionally there may be two sori, or rarely an additional one on the outer edge.

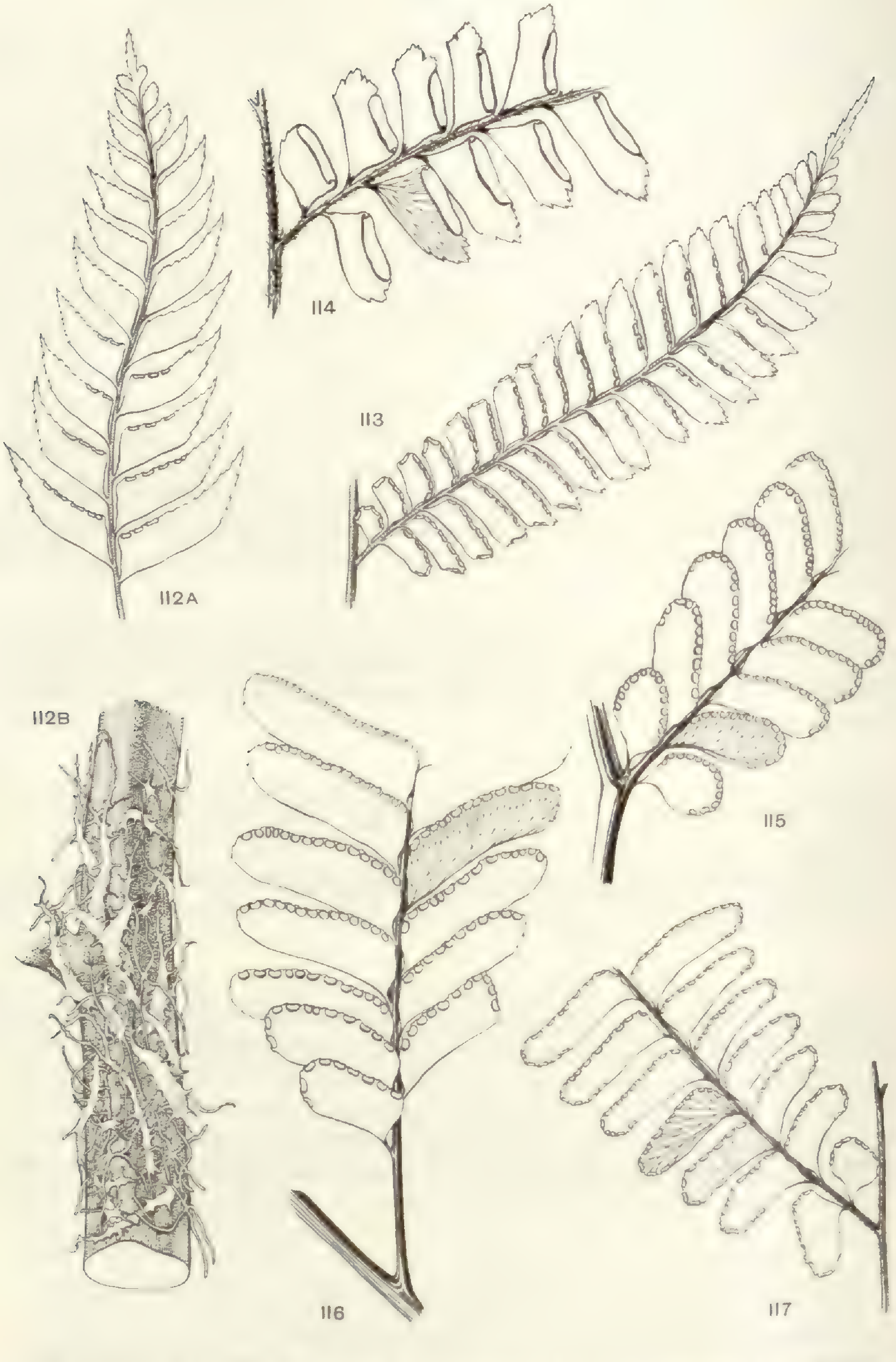
Guianas to Colombia, to Bolivia and Brazil; Mexico; West Indies.

In dense or partially open forest, Amazonas and Loreto south to Cuzco, 100-1800 m.

Selected specimens: AMAZONAS: mouth of the Río Santiago, *Mexia 6133a* (GH, NY, UC, US), *Tessman 4277* (B). LORETO: Río Itaya, *Killip & Smith 29301* (NY, US), *29339* (F, NY, US), *29431* (F, GH, NY, US); near Iquitos, *Klug 311* (F, NY, US), *1399* (F, NY, US), *Tryon & Tryon 5194* (BM, F, GH, MO, U, USM); Río Mazán, *Schunke 108* (F, GH, NY, UC, US, USM); lower Río Huallaga, *L. Williams 5299* (F). JUNIN: Polonia, Satipo, 1940, *Ridoutt* (US). CUZCO: Río Sambray, prov. Convención, *Mexia 8066* (F, GH, MO, UC, US).

20. **Adiantum tomentosum** Kl. Linnaea 18: 553. 1845. Type: British Guiana, *Schomburgk 1202*, B! fragment, GH! US! FIG. 115.

Rhizome moderately stout, rather long-creeping; leaves to ca. 1.25 m. tall, petiole dark reddish-brown to atropurpureous, more or less deciduously puberulent, the rachis persistently so; lamina ovate-deltoid or broadly so to broadly ovate-oblong, bipinnate, pinnae ca. 15-25 cm. long, pinna-rachises puberulent to pubescent on the upper side only, glabrous beneath, the terminal pinna reduced at the base, pinnules glabrous, usually imbricate, sterile ones rather coarsely but evenly serrate.



FIGS. 112-117. Fig. 112. *Adiantum tetraphyllum:* A, apex of fertile pinna, × ½, Peru, *Tryon & Tryon 5438*, MO; B, portion of pinna-rachis, enlarged, *idem.* Fig. 113. *A. fructuosum:* fertile pinna, × ½, Peru, *Tryon & Tryon 5177*, MO. Fig. 114. *A. pulverulentum:* base of fertile pinnae, × 1, Bolivia, *R. S. Williams 1321*, GH. Fig. 115. *A. tomentosum:* base of fertile pinna, × 1, Peru, *Tryon & Tryon 5295*, MO. Fig. 116. *A. macrocladum:* base of fertile pinna, × 1, Peru, *Mexia 8292*, GH. Fig. 117. *A. terminatum:* base of fertile pinna, × 1, Peru, *Klug 1270*, US.

those nearest the usually acute terminal segment moderately reduced; sori numerous, roundish to short-oblong, borne on the upper and outer edges, sometimes a few also on the inner edge.

This is one of the most distinctive species, the pinna-rachises being puberulent or short-pubescent on the upper side only. Except for the next species, it is also distinctive in its closely imbricate and very obtuse pinnules that are often curved.

Guianas to Colombia, to Peru and Brazil.

Dense forest, Loreto, Huánuco and Junín, 100-400 m.

Selected specimens: LORETO: Iquitos, *Killip & Smith 27415* (NY, US), *27490* (NY, US); near Iquitos, *Killip & Smith 29946* (NY, US); Río Nanay, *L. Williams 1065* (F), *1070* (F). HUANUCO: Tingo María, *Aguilar 301* (UC), *Tryon & Tryon 5295* (BM, F, GH, MO, NY, U, UC, US, USM). JUNIN: Puerto Bermudez, *Killip & Smith 26549* (GH, NY, US); Puerto Yessup, *Killip & Smith 26376* (F, NY, US).

21. **Adiantum macrocladum** Kl. Linnaea 18: 554. 1845. Type: Peru, *Poeppig 1147*, B! photo BM! isotypes: GH! LE! US! FIG. 116.

Adiantum Mexiae Copel. Univ. Cal. Publ. Bot. 19: 303. 1941. Type: Huánuco, Peru, *Mexia 8292*, UC; isotype: GH! US!

Rhizome moderately stout, rather long-creeping; leaves up to 1 m. tall, petiole atropurpureous, glabrous, more or less glaucous, the rachis similar but usually lighter; lamina more or less circular to broadly ovate, bipinnate above the basal pinnae, which are divided on the upper side into two to four major divisions and tripinnate, pinnae ca. 20-40 cm. long, pinna-rachises glabrous, the terminal pinna reduced at the base, pinnules glabrous, imbricate, sterile ones mostly evenly serrate, those nearest the long-acuminate terminal segment greatly reduced; sori numerous, very short-oblong, borne on the upper edge.

In the general aspect of the pinnae this species is similar to the previous, *A. tomentosum*, but the wholly glabrous pinna-rachises, in addition to the petiole and rachis, and the acroscopically branched basal pinnae easily distinguish it. The pinnules are quite long and obtuse and the sori small and numerous.

Endemic to Peru.

Dense forests, Huánuco and Junín, 340-860 m.

Specimens seen: *Poeppig 1147* (B, GH, LE, US), 1829, *Poeppig* (MO). HUANUCO: Tingo María, *Stork & Horton 9531* (F, UC); near confluence of Río Cayumba and Río Huallaga, *Mexia 8292* (GH, US). JUNIN: Cahuapanas on Río Pichis, *Killip & Smith 26790* (NY, US).

22. **Adiantum terminatum** Miq. Het. Instit. Versl. Meded. Ned. Instit. Wet. 1842: 3. 1843 (cited by C. Chr. Ind. Fil. as Diar. Inst. Reg. Bat.). Type: Bergendall, Surinam, *Focke*, U! Fig. 117.

Rhizome rather slender, short-creeping, the petiole bases approximate; leaves ca. 20-45 cm. tall, petiole dark reddish-brown to atropurpureous, deciduously pubescent-scaly, the rachis persistently so; lamina broadly deltoid to oblong or oblong-ovate, bipinnate, pinnae ca. 8-15 cm. long, pinna-rachises pubescent-scaly, the terminal pinna reduced at the base, pinnules dull green to faintly glaucous, with numerous simple trichomes beneath, sterile ones mostly coarsely and evenly serrate, those nearest the acuminate terminal segment reduced, sori several to numerous, very short-oblong, borne on the upper and often also on the outer and inner edges.

Adiantum terminatum is evidently a critical species for none of the identified material I have seen from Peru has been properly named. The numerous small sori, the pubescent-scaly rachis and pinna-rachises, the reduced apical pinnules and the pinnules with trichomes on the under surface serve to distinguish it.

Maps 31-32. Map 31, *Adiantum latifolium*. Map 32, *A. subvolubile*.

Guianas to Colombia, to Bolivia and Brazil; Guatemala; Trinidad.

In forests, Loreto and San Martín to Puno, 100-800 m.

Specimens seen: SAN MARTIN: near Tingo María, *Allard 20451* (US), *22542* (US). LORETO: near Iquitos, *Klug 1270* (NY, US); lower Río Huallaga, *L. Williams 5053* (F); Nauta, *Ferreyra 5134* (USM). HUANUCO: Tingo María, *Stork & Horton 9520* (F, UC), *Tryon & Tryon 5327* (BM, F, GH, MO, NY, U, UC, US, USM), *Allard 21505* (GH, US). JUNIN: Satipo, Aug. 1940, *Ridoutt* (GH, USM); Puente Perené, *Coronado 262* (GH, UC). PUNO: San Gaban (Río), *Lechler 2319, 2319a* (B).

23. **Adiantum humile** Kze. Linnaea 9: 80. 1834. Type: Upper Huallaga, Mission Tocache, Peru, June, 1830, *Poeppig*, LZ, destroyed. An authentic specimen: Tocache, Aug. 1830, *Poeppig*, W! may replace the holotype. FIG. 118.

Adiantum Killipii Maxon & Weath. Amer. Jour. Bot. 19: 166. 1932. Type: Ancón Hill, Canal Zone, Panama, *Killip 2752*, US!

Rhizome moderately stout, very short-creeping, the petiole bases approximate; leaves ca. 30-75 cm. tall, petiole dark reddish-brown to atropurpureous, deciduously scaly, the rachis persistently so; lamina deltoid to oblong-ovate, bipinnate, pinnae ca. 8-15 cm. long, pinna-rachises pubescent-scaly, the terminal pinna reduced, or broadest, at the base, pinnules glaucous, with usually numerous simple trichomes beneath, narrow scales sometimes also present, sterile pinnules coarsely and evenly serrate, pinnules nearest the acute to subobtuse terminal segment not much reduced; sori several, borne on the inner, upper and outer edges.

British Honduras to Panama; French Guiana and Trinidad to Colombia and south to Peru; Brazil.

In forest, San Martín and Junín, 500-700 m.

Specimens seen: SAN MARTIN: Tocache, *Poeppig* (W). JUNIN: Quimiri Bridge, La Merced, *Killip & Smith 24003* (NY, US).

24. **Adiantum cayennense** Kl. Linnaea 18: 552. 1845. Type: Herb. Willd. 20084, B! photo GH; paratype: British Guiana, *Schomburgk 1201*, B! FIG. 119.

Rhizome moderately stout, rather short-creeping; leaves ca. 80-100 cm. tall, petiole dark reddish-brown to atropurpureous, more or less persistently pubescent-scaly, the rachis densely and persistently so; lamina ovate-deltoid to ovate or oblong-ovate, bipinnate, pinnae ca. 15-20 cm. long, pinna-rachises densely pubescent-scaly, pinnules glabrate or scaly beneath, sterile ones coarsely and often unevenly serrate, those nearest the broadly acute to acuminate terminal segment greatly reduced; sori several to numerous, oblong, borne on the upper and outer edges, often a few on the inner edge.

This species is closely related to the two preceding ones; however, it has the pinnules glabrous or only with a few scales beneath, while *A. terminatum* and *A. humile* have the pinnules with simple trichomes beneath.

Guianas to Colombia, Peru and Brazil.

In forests, Loreto, San Martín and Huánuco, 135-800 m.

Specimens seen: SAN MARTIN: east of Tingo María *Allard 21623* (US). LORETO: Balsa Puerto, lower Río Huallaga basin, *Killip & Smith 28510* (NY, US); below Yurimaguas, *Killip & Smith 28785* (NY, US); lower Río Huallaga, *L. Williams 4133* (F, US). HUANUCO: Tingo María, *Tryon & Tryon 5276* (BM, F, MO, USM).

25. **Adiantum pectinatum** Ettingsh. Farnkr. 85, t. 45. figs. 14-16. 1865. Type: Goyaz, Brazil, *Pohl 1481*, W!; isotype: B! *(s.n.)*, GH! FIG. 120.

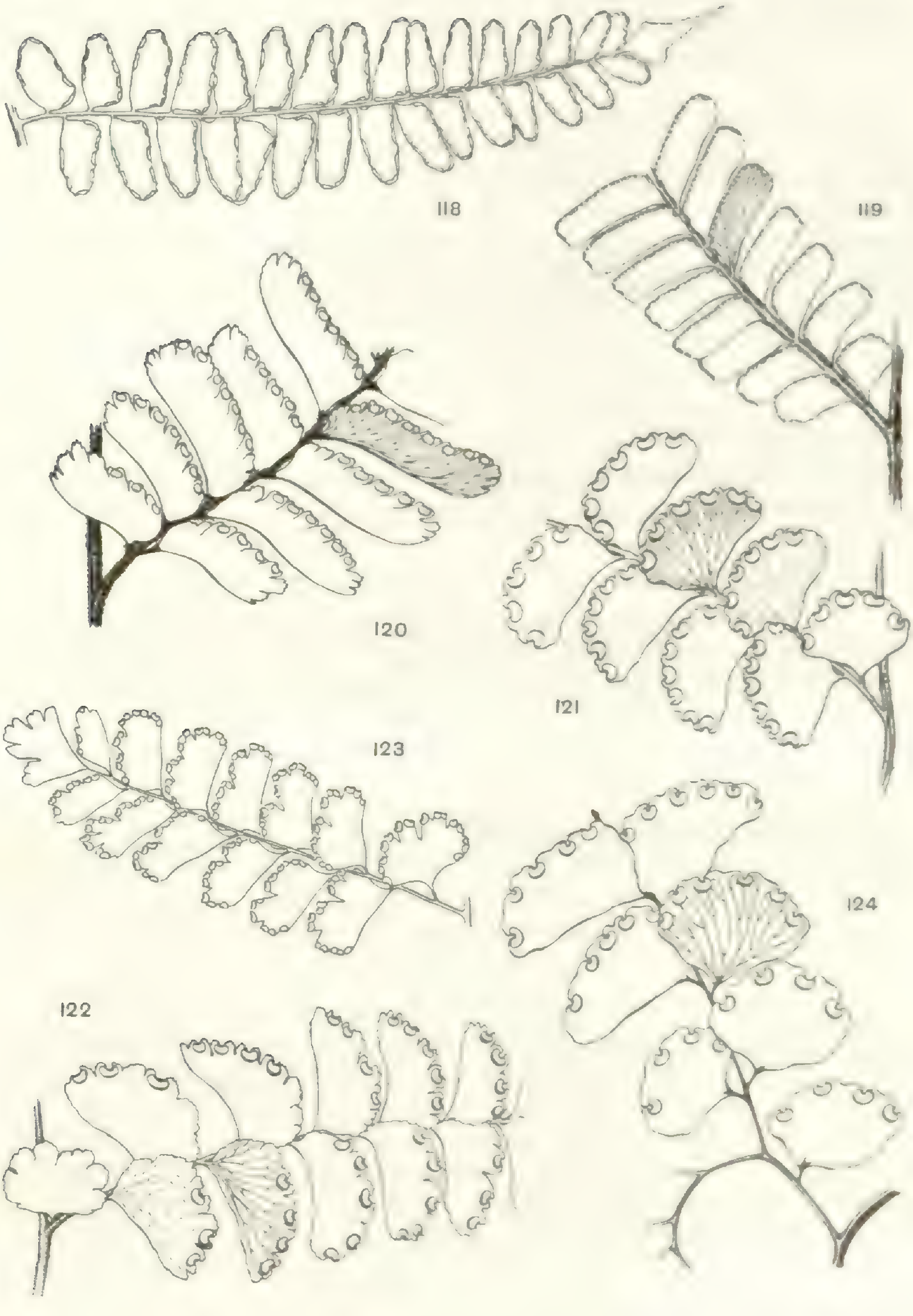
Rhizome very stout, moderately creeping; leaves very large, up to 2 m. tall or more, petiole very stout (to nearly 1 cm. in diameter at the base), dark reddish-brown to atropurpureous, deciduously pubescent-scaly, the rachis rather persistently so; lamina broadly deltoid-ovate to deltoid-circular, 4- to 5-pinnate, rarely 6-pinnate, the basal pinnae largest, pinnae widely alternate, 30-90 cm. long, pinna-rachises pubescent-scaly, ultimate segments glabrate or slightly scaly beneath, sterile ones deeply incised-lobed, those nearest the rather obtuse to acute terminal segment of the penultimate segments moderately to greatly reduced; sori several, roundish to lunate, borne on the upper and sometimes also a few on the outer edge.

This species is characterized by the deeply incised pinnules, or ultimate segments, and the highly divided lamina that is commonly 4- to 5- pinnate at the base. It is the largest of the Adiantums, some leaves reaching a length of at least 2 m. It differs from the related *A. polyphyllum* Willd., with which it has been confused, in having the several sori borne only on the upper edge of the pinnules and in having the stipe, rachis and pinna-rachises pubescent-scaly rather than glabrous.

Costa Rica to Argentina and Brazil.

In woods and dense forests, San Martín to Cuzco, 700-2000 m.

Selected specimens: SAN MARTIN: Moyabamba to Huallaga, *Stübel 1091* (B); Tarapoto, *Spruce 4781* (K). HUANUCO: Pampayacu, *Kanehira 130* (GH); Muña, *Pearce 552* (K). JUNIN: La Merced, *Soukup 1082* (F), *3405* (GH, US), *Killip & Smith 23448* (GH, NY, US), *Tryon & Tryon 5437* (BM, F, MO, U, US, USM). CUZCO: Torontoy, *Herrera 1297* (US); Chaupimayo, *Bües 1292* (US); Bajios de Rosalina, prov. Convención, *Vargas 12289* (GH).



FIGS. 118-124. Fig. 118. *Adiantum humile:* fertile pinna. × ½, Panama, *Killip 12068*, GH. Fig. 119. *A. cayennense:* basal portion of fertile pinna. × 1, Peru, *Killip & Smith 28785*, US. Fig. 120. *A. pectinatum:* base of fertile pinna, × 1, Peru, *Soukup 3405*, GH. Fig. 121. *A. sessilifolium:* base of fertile pinna, × 1, Peru, *Osgood 67*, US. Fig. 122. *A. Henslovianum:* base of fertile pinna, × 1, Venezuela, *Fendler 78*, GH. Fig. 123. *A. lobatum:* fertile pinna: × ½, Peru, *Correll & Smith P801*, GH. Fig. 124. *A. patens:* base of fertile pinna and portion of rachis, × 1, Venezuela, *Fendler 79*, GH.

26. **Adiantum sessilifolium** Hook. Sp. Fil. 2: 44, t. 85B. 1851. Type: Chachapoyas, Peru, *Mathews 1855*, K! photo GH. FIG. 121.

Adiantum Henslovianum var. *macrosora* Hieron. Hedwigia 48: 238. 1909. Syntypes: Peru, *Stübel 1031, 1046* B!

Rhizome rather small, short-creeping; leaves ca. 15-30 cm. tall, petiole dark straw-colored to dark reddish-brown, more or less persistently short-pubescent, the rachis definitely so; lamina elongate-deltoid, bipinnate, pinnae ca. 2-6 cm. long, the terminal one broadest at the base, pinna-rachises whitish short-pubescent, pinnules (and undivided pinnae) whitish-pubescent beneath, sterile ones moderately lobed, those nearest the obtuse to broadly rounded terminal segment not much reduced, the basal pinnule of the upper pinnae overlying the rachis; sori few, oblong-lunate to reniform, borne on the upper and outer edges.

Endemic to Peru.

Rocky slopes and among rocks of Inca walls, Cajamarca and Amazonas to Cuzco, 2000-2700 m.

Specimens seen: CAJAMARCA: west of Balsas, *Osgood & Anderson 67* (F), *Osgood 67* (US); Celedín, *Stübel 1046, 1046a* (B); 40 km. from Cajamarca on road to Chilete, *Correll & Smith P842* (GH). AMAZONAS: Chachapoyas, *Mathews 1855* (K); Leimebamba, *Stübel 1031* (B). LIBERTAD: between Alpamarca and Retamas, prov. Pataz, *López & Sagástegui 3634* (GH). HUANUCO: Muña, *Bryan 428* (F, GH). CUZCO: about Cuzco, 1854, *Wm. Lobb* (BM).

27. **Adiantum Henslovianum** Hook. f. Trans. Linn. Soc. Lond. 20: 169. 1847. Syntypes: Galápagos Isls., *Darwin*: James Is. CGE, tracings GH; Charles Is. K! photo GH. FIG. 122.

Adiantum laetum Kuhn, Linnaea 36: 76. 1869. Type: Chachapoyas, Peru, *Mathews 3295;* isotype: K! photo GH, US.

Rhizome rather small, very short-creeping; leaves ca. 40-90 cm. tall, petiole light to rather dark reddish-brown, glabrate to puberulent, the rachis puberulent; lamina more or less ovate, bipinnate, pinnae ca. 6-15 cm. long, the terminal pinna broadest at the base, pinna-rachises puberulent, pinnules whitish-pubescent beneath, or slightly so, sterile ones moderately lobed, those nearest the acute to broadly rounded terminal segment greatly reduced or not, the basal pinnule of at least the upper pinnae overlying the rachis; sori few, roundish, lunate or reniform, borne on the upper and outer edges.

The flabellate-cuneate upper basal pinnules that are borne very close to the rachis so that they overlap it, the nearly sessile pinnae and the puberulent rachis and pinna-rachises serve to distinguish this species. The pinnules are delicate in texture.

Venezuela to Ecuador and Peru.

Rocky slopes, Lambayeque and Amazonas, ca. 1500 m.

Specimens seen: LAMBAYEQUE: 31 km. from Olmos on road to Jaén, *Correll & Smith P807* (GH). AMAZONAS: Chachapoyas, *Mathews 3295* (K).

28. **Adiantum lobatum** Presl, Rel. Haenk. 1: 62, t. 10, f. 4. 1825. Type: Guayaquil, Ecuador, 1790, *Haenke*, PR, photo GH. FIG. 123.

Rhizome rather slender, short-creeping, the petioles spaced but not distant; leaves to 60 cm. tall, petiole atropurpureous, glabrous; lamina deltoid to long-triangular, bipinnate to tripinnate, rachis and pinna-rachises minutely puberulent on the upper side, terminal pinna somewhat reduced at the base, ultimate segments glabrous, mostly oblong to trapeziform, the basal ones more or less flabellate, entire to sometimes rather strongly incised, stalks very short to usually short, the dark color entering the base of the segment, sterile vein-tips end between indistinct marginal crenulations; sori orbicular to suborbicular, borne on the upper and outer edges.

Ecuador and Peru.
Brushy and rocky hillsides, Lambayeque, 1250-1400 m.

Specimens seen: LAMBAYEQUE: 27 km. from Olmos on road to Jaén, *Correll & Smith P801* (GH, LL, US); 31 km. from Olmos on road to Jaén, *Correll & Smith P808* (GH, LL).

29. **Adiantum patens** Willd. Sp. Pl. 5: 439. 1810. Type: Caracas, Venezuela, *Bredemeyer* (Herb. Willd. 20078), B! photo GH; isotype: W! FIG. 124.

Rhizome rather small, short-creeping; leaves ca. 20-45 cm. tall, petiole light to dark reddish-brown, glabrous or slightly puberulent, rachis (or rachises) similar; lamina deltoid-ovate to nearly circular, bi- to tripinnate, penultimate segments on the upper side of each part of the divided rachis, or the lamina more or less pinnate in division and the terminal pinna somewhat reduced at the base, penultimate segments ca. 11-15 cm. long, their axes glabrous to puberulent, rarely short-pubescent, ultimate segments glabrous beneath, or rarely whitish short-pubescent, sterile ones moderately lobed, or evenly serrate, those nearest the broadly rounded terminal segment reduced or not, the basal ultimate segments hardly or not overlying the adjacent axis; sori few, roundish, lunate or reniform, borne on the upper and outer edges.

The manner of division of the lamina is similar to that in *A. pedatum* of North America, that is the rachis is divided and the pinnae arise only from the acroscopic side of each of the two branches. This character alone will identify the species; however, in small or poorly developed leaves the lamina may be essentially pinnate and then the glabrous rachis and pinna-rachises (rarely the latter are partially puberulent) must serve to distinguish it from the preceding species.

Venezuela and Colombia to Bolivia; Mexico.

In woods or on shaded rocks, Tumbes to Lambayeque and Cuzco, 150-2050 m.

Specimens seen: TUMBES: between Cancho and Cotrina, *Coronado 233* (GH). PIURA: Talara, *Haught 92* (US); Huancabamba, *Ferreyra 10877* (GH, USM). LAMBAYEQUE: prov. Lambayeque, *López et al. 4045* (GH); Olmos to Jaén, *Correll & Smith P806* (GH). CUZCO: Machu-Picchu, *Vargas 3352* (MO, US).

30. **Adiantum Capillus-Veneris** L. Sp. Pl. 2: 1096. 1753. Type: LINN 1252. 9 chosen by Pichi-Sermolli in Webbia 12(2): 678. 1957. FIGS. 94, 125.

Rhizome rather slender, short- to long-creeping; leaves ca. 15-45 cm. tall, petiole reddish-brown to atropurpureous, glabrous, or slightly scaly at the base, rachis similar, glabrous; lamina elongate-deltoid to ovate to elongate-ovate, bi- to tripinnate, pinnae stalked, ultimate segments cuneate-flabellate to suborbicular, rather symmetrical or not, glabrous beneath, not articulate, the color of the apex of the stalk passing into the base, sterile margins with a cartilaginous border, each vein ending in a tooth; sori few, rather squarish to oblong.

The Peruvian material is evidently identical to the European. It is distinct among other Peruvian species by the pronounced cartilaginous border of the segments, the light grayish-brown rhizome scales and the veins that each end in a tooth on the sterile margins.

Adiantum Capillus-Veneris is unique among Peruvian ferns in having its distribution restricted to the coastal portion of the Department of Lima and a valley in Ica. Its close correlation with city, suburban and resort areas strongly suggests that it has been introduced as a garden plant and become locally naturalized.

Tropical and temperate America; Old World.

Damp, gravelly sea cliffs, banks of irrigation ditches and local seepage areas, Lima and Ica, sea level to 2000 m.

Selected specimens: LIMA: Lomas de Amancaes, *Ferreyra 6257* (USM); Laguna de Villa, *Coronado 4* (GH, MO, UC, US); Choisica to Matucana, *Vargas 4774* (UC); Miraflores, *Tryon & Tryon 5216* (BM, F, GH, MO, U, UC, US, USM); Chorrillos, *Tryon & Tryon 5460* (BM, F, MO, U, USM). ICA: Huamani, collector unknown (USM).

31. **Adiantum subvolubile** Kuhn, Linnaea 36: 77. 1869. Type: Puento de Baños, Ecuador, *Spruce 5318*, B!; isotypes: BM! GH! K! FIG. 126, MAP 32.

Rhizome rather slender, moderately long-creeping, with tufts of petiole bases borne at intervals; leaves ca. 20-60 cm. long, petiole light to dark reddish-brown, glabrous or slightly scaly at the base, rachis similar, glabrous; lamina more or less elongate-ovate, bipinnate, or tripinnate in the center, pinnae subsessile, the basal pinnule undivided, overlying the rachis, basal pinnae often reduced or withered, ultimate segments cuneate-flabellate or broadly so to suborbicular, rather symmetrical or not, glabrous beneath, not articulate, the color of the apex of the stalk passing into the base, sterile margins with each vein ending in a usually well developed sinus; sori few, roundish to lunate to nearly reniform.

This species is characterized by the subsessile pinnae with the inner pinnule borne very close to the rachis and overlapping it. It differs from the related *A. excisum* of Chile in having a glabrous rather than a deciduously scaly rachis. In addition *A. excisum* is a smaller and more delicate species and has large, thin, pale brown scales at the base of the petiole. *Adiantum subvolubile* has been more frequently confused with *A. concinnum*, a common species northward, but differs in the character of the inner upper pinnules of the lower pinnae mentioned in the key.

Ecuador and Peru.

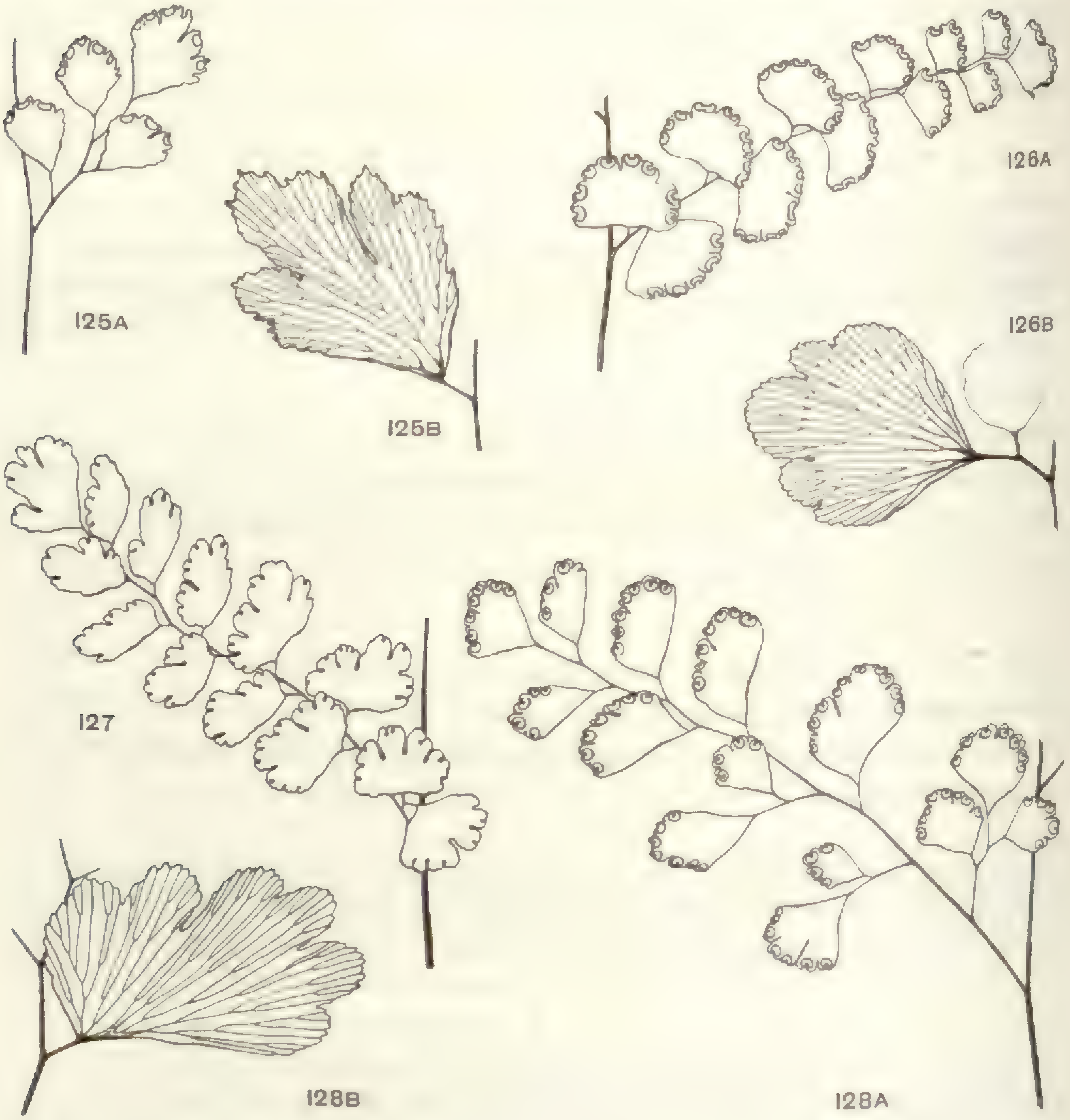
Adiantum subvolubile is one of the characteristic ferns of the coastal lomas. In crevices of rocks, or at the base of rocks, less often on the ground, Piura to Cuzco and Moquegua, 50-3000 m.

Selected specimens: PIURA: Canchaque, *Ferreyra 3095, 10813* (USM). CAJAMARCA: Summit of Cerro Prieto, *Haught 280* (US). LIBERTAD: Lomas de Viru, *Coronado 283* (GH, UC); Lomas Campana, *Coronado 282* (GH, UC). ANCASH: Lomas de Mongon, *Coronado 303* (GH, UC). LIMA: Loma de Atacongo, *Pennell 14762* (F, GH, NY, PH), *Ferreyra 2440* (BM, GH, USM); Loma de Lachay, *Coronado 24* (UC, US); Loma de Amancaes, *Coronado 13* (GH, MO, UC, US), *Tryon & Tryon 5214* (BM, F, MO, U, US, USM); Río Chillón, above Obrajillo, *Pennell 14368* (F, GH, NY, PH); Lomas de Quilmaná, *Coronado 28* (UC, US); Lomas de Mongomarca, *Velarde (Coronado 19)* (GH, UC, US); Lomas de Pativilca, *Coronado 308* (GH). HUANUCO: Gorge of Río Chinchao, *Tryon & Tryon 5315* (BM, F). CUZCO: Sicuani, *D. Stafford 419* (BM). AREQUIPA: Mollendo, *I. M. Johnston 3573* (GH, US); Lomas de Capac, *Coronado 38*

(UC, US); slope of Pichu-Pichu, *Sandeman 3833* (K). MOQUEGUA: Ilo, *D. Stafford 931* (BM).

32. **Adiantum concinnum** Willd. Sp. Pl. 5: 451. 1810. Type: Caracas, Venezuela, *Humboldt & Bonpland* (Herb. Willd. 20099), B! photo GH. FIG. 127.

Rhizome moderately slender, rather short-creeping, often multicipital; leaves ca. 20-80 cm. tall, petiole reddish-brown to atropurpureous, glabrous or slightly scaly at the base, rachis similar, glabrous; lamina ovate-oblong to linear-lanceolate, bipinnate (except at the very base) to generally tripinnate, pinnae subsessile, the basal pinnule divided into two ultimate segments, at least at the base of the blade, overlying the rachis, ultimate segments cuneate-flabellate to broadly so to suborbicu-



FIGS. 125-128. Fig. 125. *Adiantum Capillus-Veneris:* A, fertile pinna, × ¾, Peru, *Tryon & Tryon 5216*, MO; B, sterile ultimate segment, × 1½, *idem.* Fig. 126. *A. subvolubile:* A, fertile basal pinna, × ¾, Peru, *Grant 7444*, GH; B, sterile ultimate segment, × 1½, Peru, *Coronado 289*, GH. Fig. 127. *A. concinnum:* basal pinna, × ¾, Peru, *Coronado 229*, GH. Fig. 128. *A. Raddianum:* A, fertile basal pinna, × ¾, Peru, *Coronado 157*, GH; B, sterile ultimate segment, × 1½, Peru, *J. B. Steere*, GH.

lar, rather symmetrical or not, glabrous beneath, not articulate, the color of the apex of the stalk passing into the base, sterile margins with each vein ending in a sinus; sori few to several, roundish to lunate to reniform.

The differences from the closely related *A. subvolubile* are discussed under that species.

Venezuela to Ecuador and adjacent Peru; to Mexico; West Indies.

In woods and along irrigation ditches, Tumbes to Cajamarca, 200-2200 m.

Specimens seen: TUMBES: between Tumbes and Cancho, *Coronado 229* (GH, UC); between Cancho and Cotrina, *Coronado 222* (GH, UC). PIURA: cerca a Chanchaque, *Ferreyra 10813* (GH, USM). LAMBAYEQUE: 20 km. from Olmos on road to Jaén, *Correll & Smith P791* (GH). CAJAMARCA: alrededores de San Benito, prov. Contumazá, *Sagástegui 3742 1/2* (GH).

33. **Adiantum Raddianum** Presl, Tent. Pterid. 158. 1836, based on Raddi, Pl. Bras. 1: t. 78, f. 2. 1825. FIG. 128, MAP 33.

Adiantum cuneatum Langsd. & Fisch. Ic. Fil. 23, t. 26. 1810, not Forst. 1786. Type: Ins. St. Catharina, Brazil, *Langsdorff*, LE! photo GH! isotype: BM!

Adiantum colpodes Moore, Gard. Chron. 1865: 530. Type: Ecuador, *Pearce; Cult. Chelsea*, Herb. Moore, K! photo GH.

Adiantum tinctum Moore, Gard. Chron. 1862: 932. Type: Peru, *Hort. Veitch*, K! photo GH.

Adiantum rubellum Moore, Gard. Chron. 1868: 866. Type: Bolivia, *Hort. Veitch*, K! photo GH.

Adiantum decorum Moore, Gard. Chron. 1869: 582. Type: Peru, *Pearce*, K! photo GH.

Adiantum Moorei Baker, Gard. Chron. 1873: 811, based on *A. amabile* Moore, Gard. Chron. 1868: 1090, not Liebm. 1849. Type: Peru, *Pearce*, K! photo GH.

Adiantum rufopunctatum Kuhn, Jahrb. Bot. Gart. Berlin 1: 350. 1881. Type: evidently Yungas, Bolivia, *D'Orbigny 165*, B!; isotype: P, photo GH, US.

Adiantum boliviense Christ & Rosenst. Fedde Rep. Spec. Nov. 5: 230. 1908. Type: Bolivia, *Buchtien 459* S-PA!; isotype: P! US!

Adiantum Remyanum Espinosa, Bol. Mus. Nac. (Santiago, Chile) 15: 96, t. 3. 1936.

Rhizome rather stout, very short-creeping, multicipital; leaves ca. 15-55 cm. tall, petiole dark reddish-brown to blackish, glabrous or slightly scaly at the base, rachis similar, glabrous; lamina elongate-triangular to lance-ovate, broadly ovate or deltoid, commonly tripinnate, less often bipinnate or quadripinnate, pinnae stalked, ultimate segments cuneate and symmetrical to broadly cuneate-flabellate and asymmetrical, glabrous or with sessile glands beneath, not articulate, the color of the apex of the stalk passing into the base, sterile margins with each vein ending in a more or less well developed sinus, sori few to several, roundish to suborbicular-reniform.

An entirely satisfactory treatment of this species or species complex must await monographic study. There are four variants within the species in Peru that, on some grounds, might warrant specific recognition but, on others, seem to represent minor variations. The characters concerned are not of the same value as in related species and are more variable and not as well correlated as one would like. Two of the variants have small segments that are cuneate and the lamina is usually tripinnate. One of these elements, to which the name *A. Raddianum* evidently should be strictly applied, has glabrous segments, while the other, which is *A. rufopunctatum*, is glandular beneath. The other variants have the segments larger and asymmetrically or broadly cuneate and the lamina often bipinnate. One, probably *A. colpodes*, is glandular beneath, and the other, *A. tinctum*, is glabrous.

The glandularity is variable and may be present or absent in a single collection, for example, *Tryon & Tryon 5446*. Leaves with large asymmetrical segments and small, cuneate, symmetrical ones both occur in *Macbride & Featherstone 1435* and *Tryon & Tryon 5368* (the small-segment kind at F). *Tryon & Tryon 5376* is also variable in the segments and one plant (at F) has bipinnate leaves, the others being tripinnate. These last two collections, both made at Potrero, include most of the variability of the segments and the complexity of the lamina. The variation in these characters is comparable to that in *A. Orbignyanum* and *A. Poiretii* var. *Poiretii*.

Adiantum Raddianum may be separated from the related *A. Poiretii* by its orbicular to suborbicular sori and its short-creeping rhizome with the petioles always closely clustered.

Tropical America.

In forests, open woods, thickets, rocky banks and cliffs, border of irrigation ditches, Tumbes and Amazonas to Cuzco, 600-4000 m.

Selected specimens: TUMBES: El Cancho to Cotrina, *Coronado 233* (UC). CAJAMARCA: Hacienda Limón, w. of Balsas, *Osgood & Anderson 58* (F); El Puquio, Guzmango, *Sagástegui 3917* (GH). AMAZONAS: Poma Cocha, *Steere* (GH). SAN MARTIN: Tarapoto, *Spruce 4664* (K); near Tingo María, *Allard 21133* (US). LIBERTAD: Samne, prov. Otuzco, *Angulo 1426* (GH). ANCASH: Llamac, *Cerrate 2367* (USM); Huasta, *Cerrate 2442* (GH, USM). HUANUCO: Mito, *Macbride & Featherstone 1435* (F, GH, US); Carpish, *Coronado 80* (GH, UC, US). LIMA: San Buenaventura, *Pennell 14559* (F, GH, NY, PH, US). JUNIN: La Merced, *Soukup 2570* (F, US, USM), *2571* (US, USM); 12 km. sw. of San Ramón, *Tryon & Tryon 5446* (BM, F, MO, U, US, USM). HUANCAVALICA: a 4 km. de Conaica, *Tovar 979* (GH, USM). APURIMAC: Quisapata, *Vargas 8898* (UC); Chincheros, *West 3694* (MO, UC). CUZCO: Potrero, near Quillabamba, *Tryon & Tryon 5368, 5376* (BM, F, GH, MO, U, US, USM); Saxihuamán, *Coronado 157* (GH, UC). PUNO: Juli, near Lake Titicaca, *Shepard 14* (NY).

34. **Adiantum Poiretii** Wikstr. Vet. Akad. Handl. 1825: 443. 1826, based on *Adiantum crenatum* Poir. in Lam. Encycl. Suppl. 1: 137. Sept. 1810, not Willd. March, 1810. Type: Tristan d'Acunha, *Petit-Thouars*, (Herb. Jussieu no. 1427) P!

MAPS 33-34. Map 33, *Adiantum Raddianum*. Map 34, *A. Poiretii* var. *Poiretii*.

Rhizome slender, rather long-creeping, with tufts of petioles borne at intervals; leaves ca. 20-50 cm. tall, petiole light or dark reddish-brown to atropurpureous, glabrous or slightly scaly at the base, rachis similar, glabrous or rarely slightly ceraceous; lamina elongate-deltoid, to broadly ovate-deltoid, tripinnate (rarely bi- or quadripinnate), pinnae stalked, ultimate segments cuneate- to subcordate-flabellate, mostly suborbicular, rather symmetrical, glabrous or occasionally ceraceous or glandular-pubescent beneath, not articulate, the color of the apex of the stalk passing into the base, sterile margins with each vein ending in a more or less well developed sinus; sori few, oblong to long-lunate, or the smallest ones roundish.

The many orbicular to suborbicular segments with oblong to lunate sori and the slender, long-creeping rhizome with loose clusters of petioles borne at intervals distinguish this species from the previous one; it differs from the next, *Adiantum Orbignyanum,* by the articulate segments and orbicular to suborbicular sori of that species. *Adiantum chilense* differs principally in having the rhizome scales and those of the petiole bases entire while in *A. Poiretii* they are freely to rather slightly ciliate.

Pichi-Sermolli (Webbia 12: 693-695. 1957) considers the Tristan d' Acunha plant to be a distinct species and restricts the name *A. Poiretii* to it. The widespread tropical species, then, bears the name *A. thalictroides* Schlecht. However, until a thorough study is made of the variations of such a widespread species as *A. Poiretii,* it does not seem advisable to accept the validity of a local segregate.

Adiantum sulpureum does not seem to be specifically separable because it agrees with *A. Poiretii* except for the characters of indument. *Adiantum Poiretii* commonly has yellow wax among the sporangia and this condition grades into the one where the wax is distributed over the segment surface.

Mexico and West Indies to Chile and Argentina; Old World.

Wooded hillsides, open woods, thickets, lomas and a variety of rocky habitats, Amazonas to Arequipa and Puno, 400-4000 m.

34a. **Adiantum Poiretii var. Poiretii.** FIG. 129, MAP 34.

Segments glabrous or often with yellow wax among the sporangia.

Mexico and West Indies to Bolivia and Uruguay.
Amazonas to Puno, 1500-4000 m.

Selected specimens: AMAZONAS: Conila, *Soukup 4166* (US); Chachapoyas, 1838, *Mathews* (K). LIBERTAD: between Huamachuco and Cajabamba, *Correll & Smith P918* (GH). ANCASH: cerca a Llamac, *Cerrate 2371* (GH, USM); Huasta, *Cerrate 2465* (GH, USM). HUANUCO: Muña, *Macbride 3932* (F, US); Mitotambo, *Ferreyra 10382* (GH, USM). LIMA: Churín, *Ferreyra 5356* (GH, USM); Tupe, *Cerrate 1078* (GH, USM). JUNIN: 10 km. east of Huancayo, *Tryon & Tryon 5468* (BM, F, MO, U, US, USM); Huacapistana, *Ferreyra 11303* (GH, USM). HUANCAVELICA: Andaimarca, *Tovar 1816* (GH, USM); Salcabamba, *Tovar 3624* (GH, USM). AYACUCHO: between Huanta and Río Apurímac, *Killip & Smith 22320* (F, NY, US). CUZCO: near town of Machu-Picchu, *Tryon & Tryon 5403* (BM, F, MO, U, US, USM); Paucartambo, *Vargas 4359* (MO, UC), *Bües 4339* (US). PUNO: Salcedo, *Soukup 1* (F, GH, UC, US). AREQUIPA: slopes of Chachani, *Sandeman 3828* (K).

34b. **Adiantum Poiretii** var. **sulphureum** (Kaulf.) Tryon, Amer. Fern Jour. 47: 139. 1957.

Adiantum sulphureum Kaulf. Enum. Fil. 207. 1824. Type: Chile, *Chamisso*, LE! photo GH; isotype: P! photo GH.

Adiantum Williamsii Moore, Gard. Chron. 10: 45, f. 4. 1878. Type: Mts. of Peru, 12,000 ft., *Williams*.

The under surface of the segments is sparingly to abundantly covered with yellow wax and also with a few to many, short to moderately long, gland-tipped trichomes.

Peru to Argentina and Chile.
Lomas and rocky hillsides, Ancash, Lima and Arequipa, 600-4000 m.

Specimens seen: ANCASH: Chiquián, *Cerrate 789* (USM). LIMA: Chicla, 1882, *Ball* (GH); km. 75, Carretera Central, *Saunders 251, 252* (BM). AREQUIPA: Loma of Atiquipa, *Coronado 31* (GH, UC, US); Arequipa, *Pennell 13189* (F); 14 km. s. of Arequipa, *Eyerdam & Beetle 22123* (GH, UC).

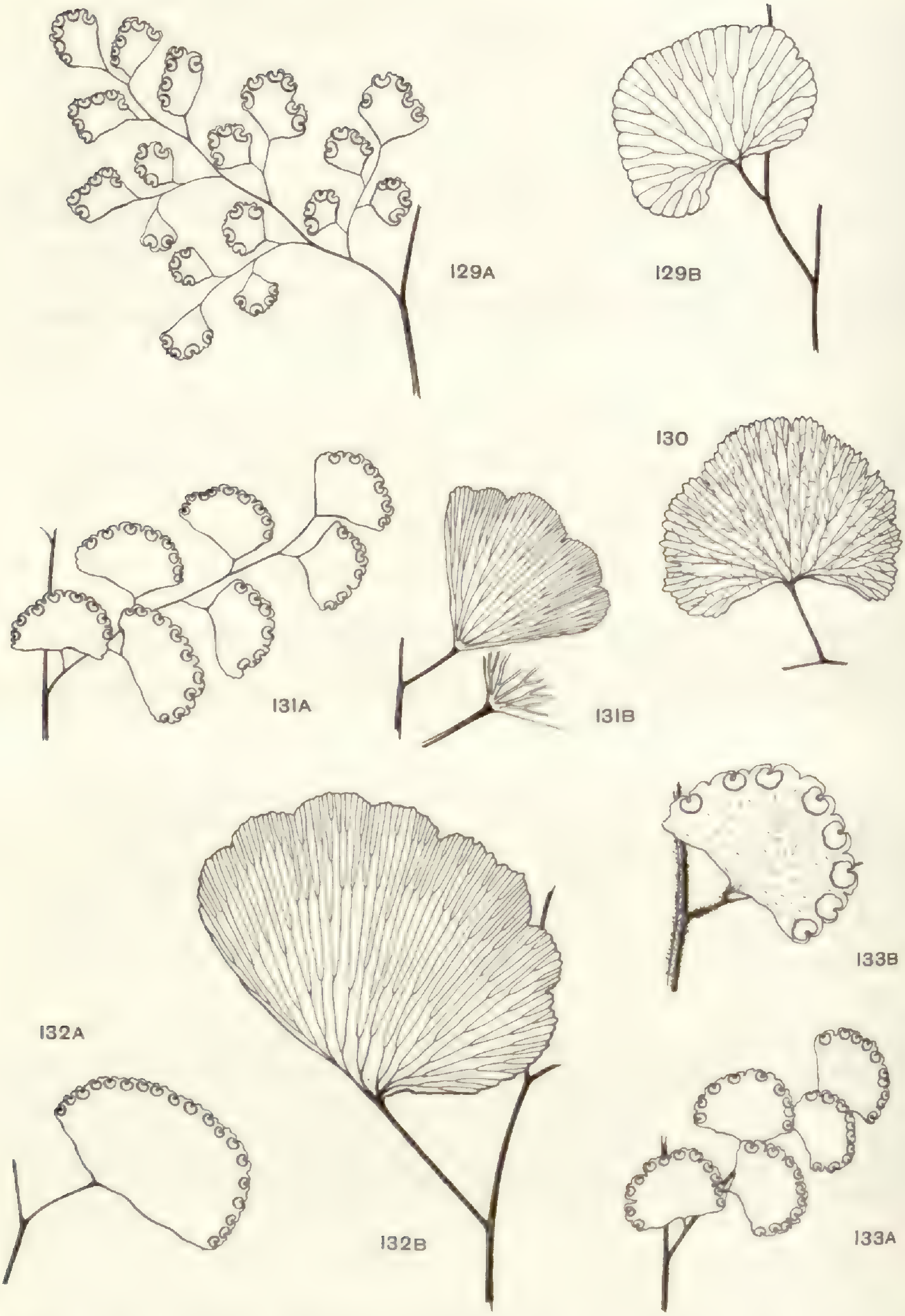
34c. **Adiantum Poiretii** var. **hirsutum** (Hook. & Grev.) Tryon, Amer. Fern Jour. 47: 141. 1957. FIG. 130.

Adiantum chilense var. *hirsutum* Hook. & Grev. Ic. Fil. 2: t. 173. 1830. Type: Chile, *Gillies*, K! photo GH.

Adiantum glanduliferum Link, Hort. Berol. 2: 18. 1833. Type: Chile, *Poeppig*; (Hort. Berol. 1846) B!

Adiantum Poiretii f. *hirsutum* (Hook. & Grev.) Hicken, Rev. Mus. La Plata 15: 261. 1908.

Adiantum Weatherbyanum Espinosa, Bol. Mus. Nac. (Santiago, Chile) 15: 93. 1936. Type: *I. M. Johnston 5307*, SGO; isotype: GH!



FIGS. 129-133. Fig. 129. *Adiantum Poiretii* var. *Poiretii:* A, fertile lower pinna, × ¾, Peru, *Hunnewell 15834*, GH; B, sterile ultimate segment, × 1½, *idem.* Fig. 130. *A. Poiretii* var. *hirsutum:* sterile ultimate segment, lower surface, × 1½. Peru. *Coronado 42*, GH. Fig. 131. *A. Orbignyanum:* A, fertile pinna, × ¾, Peru, *Cook & Gilbert 343*, US; B, pinnule, × 1½, and its base, enlarged, *idem.* Fig. 132. *A. Ruizianum:* A, fertile pinna, × ¾, Peru *Killip & Smith 25846*, GH; B, sterile pinna, × 1½, *idem.* Fig. 133. *A. imbricatum:* A, fertile upper pinna, × ¾, Peru, *Bües 1305*, US; B, fertile pinnule, × 1½, *idem.*

The under surface of the segments has long, gland-tipped trichomes and no wax.

Peru to Chile.
Lomas, Arequipa, 400-600 m.

Specimens seen: AREQUIPA: Loma de Capac, *Coronado 42* (GH, UC, US); Loma de Atiquipa, *Coronado 33* (UC, US).

35. **Adiantum Orbignyanum** Kuhn, Linnaea 36: 78. 1869. Lectotype: Bolivia, *Mandon 52,* B! photo GH. FIG. 131, MAP 35.

Rhizome slender, long-creeping, often branched, with the petioles spaced or borne in tufts at intervals; leaves ca. 15-40 cm. tall, petiole light or dark reddish-brown to atropurpureous, glabrous or slightly scaly at the base, rachis similar, glabrous; lamina lanceolate to narrowly ovate-deltoid, bipinnate to rarely tripinnate, pinnae stalked, ultimate segments cuneate-flabellate to suborbicular, rather symmetrical or not, glabrous beneath, articulated at the junction with the stalk, the apical portion of the stalk enlarged, its color abruptly distinct from that of the segment base, the segment deciduous with a sharp clean break, sterile margins with each vein ending in a usually well developed sinus; sori few to several, roundish to orbicular-reniform.

This species is clearly marked by its articulate segments; the apical portion of the segment-stalk is enlarged and the segments are decidous at that point. In addition it may be distinguished from species of similar appearance by the flabellate-orbicular to flabellate-cuneate segments, the orbicular to suborbicular sori and the inner upper pinnules especially of the upper pinnae that overlie the rachis. The rhizome is similar to *A. Poiretii* in being slender and long-creeping with loose clusters of petioles at intervals, and with scales that are slightly ciliate.

Peru and Bolivia.
Most common in open rocky places, Cajamarca to Cuzco, 2700-4000 m.

Selected specimens: CAJAMARCA: San Miguel, July 30, 1952, *A. Dias* (USM). HUANUCO: Pachachupam, Feb. 1940, *Ridoutt* (USM). JUNIN: below Palca, *Correll & Smith P766* (GH). APURIMAC: Cachora to Huillcayocc, *Vargas 9104* (UC). CUZCO: Yucay, *Herrera 714, 718, 1198* (US), *Coronado 146* (GH, UC); San Sebastian, *Pennell 13621* (F, GH, NY, PH).

36. **Adiantum Ruizianum** Kl. Linnaea 18: 551. 1845. Type: Peru, *Ruiz 26,* B! FIG. 132.

Adiantum Veitchianum Moore, Gard. Chron. 1868: 1090. Type: Muña, Peru, *Pearce,* K! photo GH.

Adiantum Steerei Harr. Jour. Linn. Soc. Lond. 16: 34. 1877. Lectotype: Poma Cocha, Peru, *Steere*, K!; isotype: GH! MO! US!
Adiantum microsorium C. Chr. Ind. Fil. 30. 1905, based on *A. Veitchianum* but an unnecessary new name as Ballard in Kew Bull. 1954 (4): 560 has pointed out.

Rhizome slender, long-creeping; leaves 15-45 cm. long, petiole dark reddish-brown to atropurpureous, glabrous or slightly scaly at the base, rachis similar, glabrous; lamina oblong or oblong-linear or oblong-tapering, 1- to bipinnate, pinnae stalked, ultimate segments broadly cuneate-flabellate to suborbicular, usually rather or quite symmetrical, glabrous, not articulate, the color of the apex of the stalk passing into the base, sterile margins with each vein ending in a more or less well developed sinus; sori several to numerous, orbicular, usually closely spaced.

Most of the material is 1-pinnate with rather large reniform to flabellate pinnae on long slender stalks; sometimes the lamina is bipinnate at the base, or even above, and then the segments may be smaller, elongate-flabellate and with

Maps 35-36. Map 35, *Adiantum Orbignyanum.* Map 36, *A. digitatum.*

short stalks. The rhizome is slender and long-creeping; occasionally the petioles are loosely clustered.

The next species, *A. imbricatum*, is closely related and the differences are discussed under it. *Adiantum Ruizianum* has frequently been confused with *A. grossum*, from which it differs in having orbicular sori rather than long-oblong or lunate ones. Also, the sterile margins have the veins ending in a sinus of (or slightly prolonged beyond) the slightly, if at all, toothed margin, while in *A. grossum* the veins run to the prominent teeth of the sharply serrate margin.

Endemic to Peru.

Damp or shaded rocky places, Amazonas, Huánuco and Junín, 1600-2900 m.

Specimens seen: AMAZONAS: Poma Cocha, *Steere* (GH, K, MO, US); Leimebamba, *Stübel 1035* (B); Cuelap, *Stübel 1019* (B). HUANUCO: Muña, *Bryan 515* (F, US), *Macbride 3942* (F, US), *Woytkowski 5223* (GH); Piedra Grande, near Río Santo Domingo, *Macbride 3709* (F, US). JUNIN: Dos de Mayo, *Killip & Smith 25846* (BM, F, GH, NY, US); Hucapistana, *Tryon & Tryon 5434* (F); Pichita Caluga, *Walden 68* (BM), *Gascoyne-Cecil 109* (BM).

37. **Adiantum imbricatum** Tryon, Amer. Fern Jour. 47: 142. t. 15. 1957. Type: La Tranca, Cuzco, Peru, *Bües 1377*, US!; isotype: CUZ! F! GH! FIG. 133.

Rhizome not seen; leaves ca. 12-30 cm. tall, petiole atropurpureous, brownish short-pubescent or glabrate, rachis similar, brownish short-pubescent; lamina long-oblong to elongate-triangular, bipinnate, basal pinnae stalked, those above short-stalked, the innermost pinnule overlying the rachis, pinna axes brownish short-pubescent, ultimate segments broadly cuneate-flabellate to suborbicular, rather to quite symmetrical, mostly imbricate, pubescent beneath, subarticulated at the junction with the stalk, the apical portion of the stalk slightly enlarged, its color abruptly distinct from that of the segment base, sterile margins not seen; sori several to numerous, roundish to orbicular-reniform, often closely spaced.

This species is related to *A. Ruizianum* but is amply distinct in a number of characters. The dark color of the segment stalk stops abruptly at the base of the segment, while in *A. Ruizianum* it enters the base of the segments; the under surface of the segments, the segment-stalks and the rachis are pubescent while in *A. Ruizianum* they are glabrous. In addition the segments have a strong tendency to be imbricate and their stalks are shorter than in *A. Ruizianum* and the lamina is often more fully bipinnate.

The somewhat similar *A. sessilifolium* has lunate sori and many of the segments are nearly sessile and the indusium is pubescent while *A. imbricatum* has orbicular sori, short-stalked segments and a glabrous indusium.

Endemic to Peru.

Rather dry, rocky places, Cuzco, 1600-2000 m.

Specimens seen: CUZCO: Puente de Collpañi, *Bües 1303* (US); La Tranca, Río Mapillo, *Bües 1305* (US), *1377* (CUZ, GH, F, US).

38. **Adiantum digitatum** Hook. Sp. Fil. 2: 38. 1851 (Presl, Tent. Pterid. 159. 1836, nomen nudum). Type: Brazil, *Sello,* K! photo GH. FIG. 134, MAP 36.

Adiantum speciosum Hook. Sp. Fil. 2: 45, t. 85C. 1851. Lectotype: Sasaranga, Ecuador, *Seemann 953,* K! photo GH.

Adiantum palmatum Moore, Gard. Chron. 1877: 40, f. 5. Type: Peru, Roezl, *ex hort. B. S. Williams,* K! photo GH.

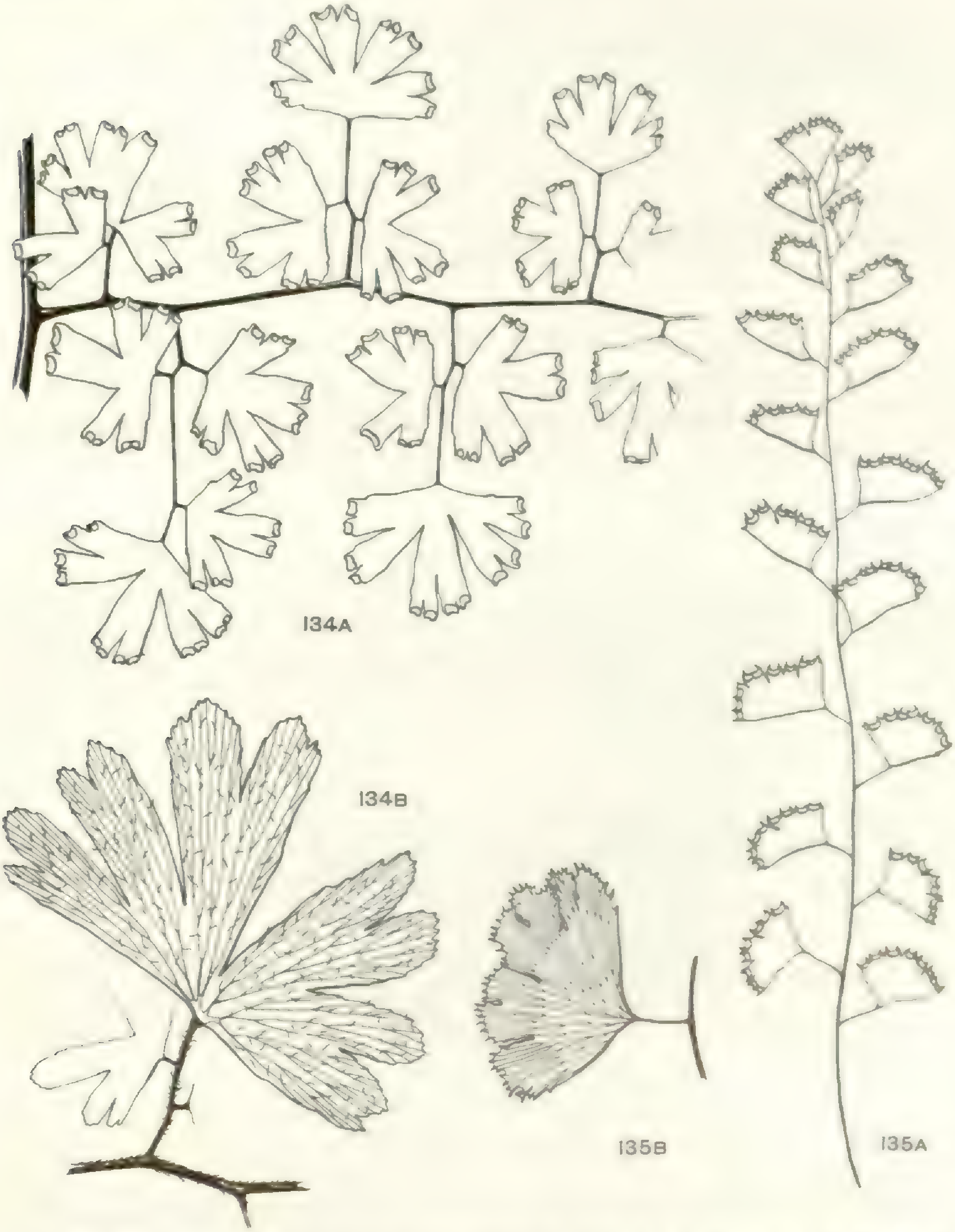
Rhizome moderately stout, long-creeping; leaves ca. 45-150 cm. tall and subscandent, petiole light to dark reddish-brown, tawny short-pubescent or glabrate, sometimes slightly scaly toward the base, rachis similar but not scaly; lamina deltoid, tripinnate or less often bipinnate, pinnae stalked, the axes tawny short-pubescent or rarely glabrate, ultimate segments more or less suborbicular, deeply cleft into about 4-7 spreading lobes, quite symmetrical or not, pubescent beneath, rarely glabrate, articulated at the junction with the stalk, the apical portion of the stalk definitely or hardly enlarged, its color abruptly distinct from that of the segment base, sterile margins with each vein ending in a tooth; sori few to several, oblong, straight or nearly so.

Adiantum digitatum is a distinctive species with its flabellate, deeply cleft segments and frequently much elongated leaf that is up to 1.5 m. in length. Most of the axes, especially those of the pinnules, are at right angles to the axis that bears them.

Ecuador to Argentina, Uruguay and Brazil.

In rocky places or at the base of rocks, in woods or brushy hillsides in soil, Tumbes to Puno, 400-4000 m. In the northern half of Peru this species is frequent on the lomas and characteristic of them.

Selected specimens: TUMBES: between Cancho and Cotrina, *Coronado 217* (GH, UC). PIURA: w. of Canchaque, *Stork 11396* (GH, US); Canchaque, *Ferreyra 10894* (GH, USM). LAMBAYEQUE: Olmos to Jaén, *Correll & Smith P829* (GH). CAJAMARCA: El Puquio, Guzmango, *Sagástegui 3915* (GH); entre Cascas y Contumazá, *López et al. 3689* (GH). LIBERTAD: Lomas Campana, *Coronado 280* (GH, UC); Lomas de Viru, *Coronado 287* (GH). ANCASH: Huasta, *Cerrate 2478* (USM). HUANUCO: Muña, *Macbride 3919* (F, GH, US); Mito, *Bryan 376* (F). LIMA: Lomas de Pativilca, *Coronado 306* (GH, UC); Lomas de Chancay, *Ferreyra 8700* (GH, USM); above San Bartolomé, *Ferreyra 9730* (GH, USM). JUNIN: 10 km. below Palca, *Walden 3, 6* (BM). CUZCO: Yucay, *Herrera 1361* (US); Vilcabamba, *Vargas 4018* (UC, US). PUNO: Ollachea, *Vargas 6917* (MO, UC, US).



FIGS. 134-135. Fig. 134. *Adiantum digitatum:* A, base of fertile pinna, × ¾, Peru, *Vargas 4018*, US; B, sterile ultimate segment, × 1½, Peru, *Vargas 6917*, MO. Fig. 135. *A. deflectens:* A, fertile lamina, × ¾, Peru, *Vargas 1658*, GH; B, sterile pinna, × 1½, *idem.*

39. **Adiantum deflectens** Mart. Ic. Crypt. Brasil. 94. 1834. Type: Santarém, prov. Pará, Brazil, *Martius*. FIG. 135.

Rhizome small, short-creeping to nearly erect; leaves ca. 15-30 cm. tall, petiole very slender, reddish-brown to atropurpureous, glabrous, rachis similar; lamina 1-pinnate, of two kinds (with rare exceptions), one oblong to very elongate-triangular, with a terminal segment, the ultimate segments (pinnae) cuneate-flabellate to broadly so, asymmetrical, moderately spaced along the rachis, the other kind linear, with a long, naked, rooting rachis-tip, the ultimate segments (pinnae) cuneate-flabellate to cuneate-ovate, nearly or quite symmetrical, widely spaced along the rachis, pinnae stalked, ultimate segments (pinnae) more or less cleft into 2-7 close lobes, glabrous, articulated at the junction with the stalk, the apical portion of the stalk enlarged, abruptly distinct in color from the segment base, sterile margins finely and sharply serrate, with each vein ending in a tooth; sori few, oblong to linear, nearly straight to long-arcuate.

This is one of the most distinctive of the Peruvian species. The lamina is 1-pinnate; the veins end in a tooth on the sterile margins; there are projecting lobes on one or both sides of the sori and the rhizome is small and short and bears slender petioles.

A number of names have been applied to this, or closely related, species, and the proper one will remain in doubt until a study is made of the whole group. *Adiantum delicatulum* Mart. (Ic. Crypt. Brasil. 93, t. 56, fig. 2. 1834) and *Adiantum dolabriforme* Hook. (Ic. Plant. t. 191. 1837) are perhaps the same species as *A. deflectens*. Other names for related species, from which *A. deflectens* appears to differ by the irregular teeth on the sterile margins, the lateral ones being variously divergent, are: *Adiantum rhizophyllum* Mart., *Adiantum filiforme* Hook., *Adiantum phillipense* L., *Adiantum lunulatum* Burm., *Adiantum flagellum* Fée and *Adiantum subaristatum* Fée.

Guianas to Colombia, to Peru, Brazil and Paraguay; to Guatemala.

Damp, shady soil, Cuzco, 820-1700 m.

Specimens seen: CUZCO: Hacienda Sahuayaco, (prov. Convención), *Bües 833* (US), *Vargas 1658, 1660* (GH); Puente de Collpañi, *Bües 1298* (US); Machu-Picchu to Quillabamba, *Mexia 8088a* (GH, MO, UC, US); Yanayaco Grande, *Bües 1035* (US); Quellouno, prov. Convención, *Vargas 13553* (GH).

TRIBE 7. PTERIDEAE

21. **Pteridium** Scop. Fl. Carn. 169. 1760. Type: *Pteris aquilina* L. = *Pteridium aquilinum* (L.) Kuhn. Fig. 136.

Terrestrial, the rhizome rather slender, extensively creeping, pubescent, bearing the leaves at intervals, leaves large to very large, tripinnate-pinnatifid to quadripinnate, glabrous to usually pubescent beneath, veins free; sporangia borne on a marginal commissure connecting the vein-tips, covered by a fertile indusium which is formed from the reflexed, modified margin, (a similar sterile indusium, not covering sporangia, present on fertile and sterile segments) an inner (true) indusium variously developed, paraphyses absent. — 1 world-wide species with 6 varieties in America, 2 of them in South America.

Tryon, R. Revision of the genus Pteridium. Rhodora 43: 1-31, 37-67. 1941, and Contrib. Gray Herb. 134. 1941.

The genus *Pteridium,* as presently interpreted, is represented by a single widely distributed species which may be

Fig. 136. *Pteridium aquilinum* var. *arachnoideum,* Inca terraces at Macchu-Picchu (Cuzco).

divided into twelve geographic varieties. Only two of the varieties occur in South America; the one represented in Peru is typically South American; the other, var. *caudatum*, is primarily Antillean but also occurs in Venezuela and Colombia and north to Mexico.

Pteridium aquilinum (L.) Kuhn, var. **arachnoideum** (Kaulf.) Brade, Zeitsch. Deut. Ver. Wissen. Kunst. São Paulo 1: 56. 1920. FIGS. 136, 137, MAP 37.

Pteris arachnoidea Kaulf. Enum. Fil. 190. 1824. Type: Brazil, *Chamisso*, LE! photo GH.

Pteridium arachnoideum (Kaulf.) Maxon, Jour. Wash. Acad. Sci. 14: 89. 1924.

Leaves to 3 m. tall, petiole usually shorter than the lamina; lamina ovate-triangular to long-triangular, to quadripinnate, free lobes present along the axes between the segments, segments arachnoid-pubescent beneath, or rarely short-pubescent or glabrous, usually having a farinaceous covering beneath the pubescence, midnerve usually with dark or bicolorous trichomes and with membranous wings along it and the veins; fertile indusium no broader than the sterile on the same segment.

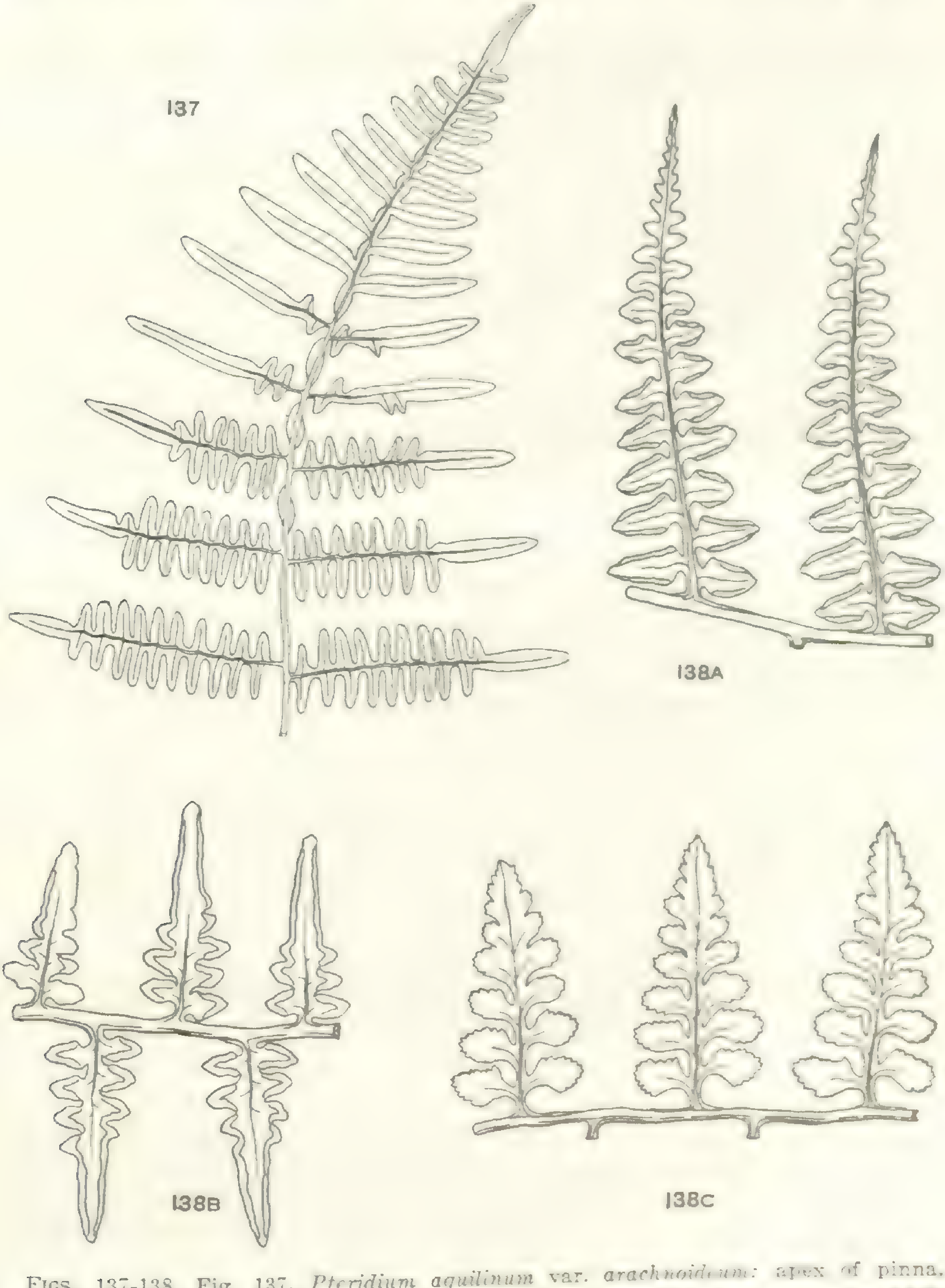
The small lobes distributed along the axes of the lamina, some of which may be attached to the base of the segment immediately above, but some of which are free, characterize var. *arachnoideum*. The related var. *caudatum* has the segments caudate but lacks the free lobes. Some specimens of var. *arachnoideum* may lack these free lobes but they have its characters of indusium and indument. The leaves of juvenile plants have a sparse, setose pubescence quite different from that of the leaves of mature plants.

Due to the nature of the rhizome and the natural vigor, this species tends to be a bad weed in agricultural areas in many parts of the world. In Peru it is locally an important weed, for example in the Cerro Azul region, in Cajamarca and elsewhere. The deep main rhizome is widely creeping and sends branches upward that in turn produce the leaves. Latent buds will renew the growth if the area is burned, cut or plowed.

South America; less common in the West Indies, Central America and Mexico.

Open slopes, thickets, pastures and cleared land, Lambayeque to Amazonas, south to Puno, 400-3000 m.

Selected specimens: LAMBAYEQUE: 20 km. e. of Olmos, on road to Jaén, *Correll & Smith P797* (GH). CAJAMARCA: nw. of Hualgayoc, *Stork & Horton 10027* (F, UC); between Cascas and Contumazá, prov. Contumazá, *López et al. 3686* (GH). AMAZONAS: alrededores de Chachapoyas, *López et al. 4342* (GH); entre Ingenio y Pomacocha, prov. Chachapoyas, *López et al. 4313* (GH). SAN MARTIN: Tarapoto, *L. Williams 5641 5971* (F). LIBERTAD: Huaranchal, prov. Otuzco, *Sagástegui 129* (GH). HUANUCO: 5 km. ne. of Acomayo, *Tryon & Tryon 5224*



FIGS. 137-138. Fig. 137. *Pteridium aquilinum* var. *arachnoideum*: apex of pinna, × ½, Ecuador, *Camp E4411*, GH. Fig. 138. *Paesia viscosa*: A. fertile pinnules, × 1, Colombia, *Killip & Smith 15923*, GH; B. fertile pinnules, × 1, Colombia, *Daniel 660*, GH; C, sterile pinnules, × 1, Colombia, *Kalbreyer 1298*, GH.

(BM, F, MO, U, US, USM); Tingo María, *Tryon & Tryon 5241* (BM, F, MO, U, US, USM). LIMA: Loma Lachay, *Ferreyra 9767* (GH, USM). JUNIN: Huacapistana, *Ferreyra 307* (GH, USM); Carpapata, *Cerrate 2796* (GH, USM). AYACUCHO: Estrella, *Killip & Smith 23095* (F, NY, US). CUZCO: Machu-Picchu, *Soukup 189* (F, GH), *Ferreyra 2705* (GH, USM); Cerro de Cusilluyoc, *Pennell 13936* (F, GH, NY, US). PUNO: Tabina, *Lechler 2031* (B).

22. PAESIA St.-Hil. Voy. Distr. Diamans 1: 381. 1833. Type: *Paesia viscosa* St.-Hil.

Terrestrial, the rhizome slender, long-creeping, pubescent, bearing the leaves at intervals; leaves small to large, bipinnate to tripinnate-pinnatifid, glabrate to glandular-pubescent, veins free; sporangia borne on a marginal commissure between the outer indusium which is formed from the reflexed, modified margin and the membranous inner (true) indusium, paraphyses absent. — 2 American species.

Paesia viscosa St.-Hil. Voy. Distr. Diamans 1: 381. 1833. Type: Serra da Piedade, Minas Geraes, Brazil, *St. Hilaire 2260*, P!; isotype: GH! FIG. 138, MAP 38.

Allosorus acclivis Kze. Farnkr. 2: 6. 1848. Lectotype: Prov. Merida,

MAPS 37-38. Map 37, *Pteridium aquilinum* var. *arachnoideum*. Map 38, *Paesia viscosa*.

Venezuela, *Funck & Schlim 1222;* isotype: GH! K! photo GH, P!

Pteris scalaris Mett. Abhandl. Senckenberg. Naturf. Ges. Frankfort 2: 282 (Uber ein. Farngatt. III: 9). 1858. Type: Spec. cult. Hort. Bot. Lips. ex Colonia Tovar, Venezuela, *Moritz 399*, Herb. Mett. B! photo GH (*Moritz 399*, B! GH! K!). *Pteris scalaris* Moritz, Bot. Zeit. 1854: 856 and *Pteris resistens* Mett. Fil. Hort. Bot. Lips. 59. 1856, *nomina nuda,* were both also "based" on *Moritz 399.*

Paesia acclivis (Kze.) Kuhn, Festsch. 50 Jub. Reals. Berlin, (Chaetopt.) 347. 1882.

Paesia scalaris (Mett.) Kuhn, *op. cit.* 347. 1882.

Pteris amazonica Christ, Hedwigia 44: 364. 1905. Type: Cerro Ponasa ("Vonasa"), Loreto, Peru, March, 1903, *Ule 6899* Herb. Christ, P!; isotype: B! photo GH, K! photo GH.

Paesia amazonica (Christ) C. Chr. Ind. Fil. 476. 1906.

Rhizome trichomes dark brown, rigid, terete or flattened in age; leaves 0.5 to ca. 2 m. long, long-petioled, lamina elongate-elliptic to long-triangular, the rachis flexuous, pinnules with the basal segment on the acroscopic side, coriaceous to herbaceous, all parts of the lamina with usually rather abundant (sometimes sparse), short, gland-tipped trichomes, sometimes also with sessile glands or with long trichomes that may be gland-tipped, or not; outer indusium thin, somewhat fimbriate or glandular-pubescent.

There is considerable variation in the shape of the segments, their texture, the density of the pubescence and the presence or absence of sessile glands, short gland-tipped trichomes or long gland-tipped trichomes. None of these characters affords a basis for the recognition of other taxa. The other American species, *P. anfractuosa* of Central America, has the basal segment on the basiscopic side of the pinnules, while *P. viscosa* has it on the acroscopic side.

It has been suggested by C. Christensen (Ark. f. Bot. 9(11) : 18-20. 1910, that *Cheilanthes glandulosa* Sw. (1817) may be a *Paesia.* If this is true, then it would be an earlier name for *P. viscosa.* A study of the material at S-PA, and the original description, leads me to the conclusion that it is more likely to be a species of *Hypolepis.*

Costa Rica; Greater Antilles; Venezuela to Colombia, south to Bolivia; Brazil.

Shrubby slopes, edge of forests and rocky places in woods, Amazonas to Puno, 1400-3600 m.

Specimens seen: AMAZONAS: Molinobamba, *Stübel 1069* (B). SAN MARTIN: Tarapoto, *Spruce 4666* (GH, K, NY, P, US). LORETO: Cerro Ponasa, (between Yurimaguas and Tarapoto), *Ule 6899* (B, K). HUAN-

UCO: Playapampa, *Macbride 4501* (F, GH, US), *4511* (F, US). CUZCO: Cerro de Cusilluyoc, *Pennell 14024* (F, GH); Calca, *Bües 1902, 1915* (US); Valle San Miquel, *Bües 2055* (US). PUNO: Tatanara, *Lechler 2536* (B).

23. LONCHITIS L. Sp. Pl. 2: 1078. 1753; Gen. Pl. 485. 1754. Type: *Lonchitis hirsuta* L.

Anisosorus Maxon. Sci Surv. Porto Rico & V. I. 6: 429. 1926, *(nom. superfl., illegit.)*. Type: the same as that of *Lonchitis*.

Terrestrial, the rhizome thick and fleshy, creeping, pubescent, bearing the leaves at close intervals; leaves large to very large, bipinnate-pinnatifid to tripinnate-pinnatifid, pubescent, veins free; sporangia borne on a marginal commissure connecting the vein-tips, covered by an indusium which is formed from the reflexed, more or less modified margin, paraphyses absent. — 1 American species.

Tryon, R. The genera Lonchitis and Blotiella, *in* Tax. Fern Notes, III. Contrib. Gray Herb. 191: 93-96. 1962.

Lonchitis hirsuta L. Sp. Pl. 2: 1078. 1753. Type: Martinique, Plumier, Fil. t. 20. FIG. 139.

Pteris laciniata Willd. Sp. Pl. 5: 397. 1810. Type: Ind. Occ. *Flügge 104* (Herb. Willd. no. 20013) B! photo GH.

Pteris lonchitoides Desv. Mém. Soc. Linn. Paris 6: 301. 1827. Type: Peru.

Pteris hirsuta (L.) J. Sm. Jour. Bot. Hooker, 4: 165. 1841, not Poir. Lam. Encycl. 5: 719. 1804.

Anisosorus hirsutus (L.) Maxon, Sci. Surv. Porto Rico & V. I. 6: 429. 1926.

Rhizome trichomes tan to brown, large, mostly flattened; leaves ca. 1-2.5 m. long, long-petioled, lamina deltoid-ovate, pinnae and pinnules often subopposite, most pinnules adnate, larger ones sessile or short-stalked, succulent (fresh) or membranous (dry), pubescent above and beneath with scattered, whitish, soft, large, multicellular trichomes; indusium membranous, sparingly pubescent, usually erose-crenulate.

Mexico and Central America; Venezuela to Colombia and south to Bolivia.

In forests, San Martín and Junín, 1300-1600 m.

Specimens seen: SAN MARTIN: Tarapoto, *Spruce 4667* (GH, K). JUNIN: Yapas, Pichis Trail, *Killip & Smith 25438* (GH, US); La Merced, *Macbride 5652* (US).

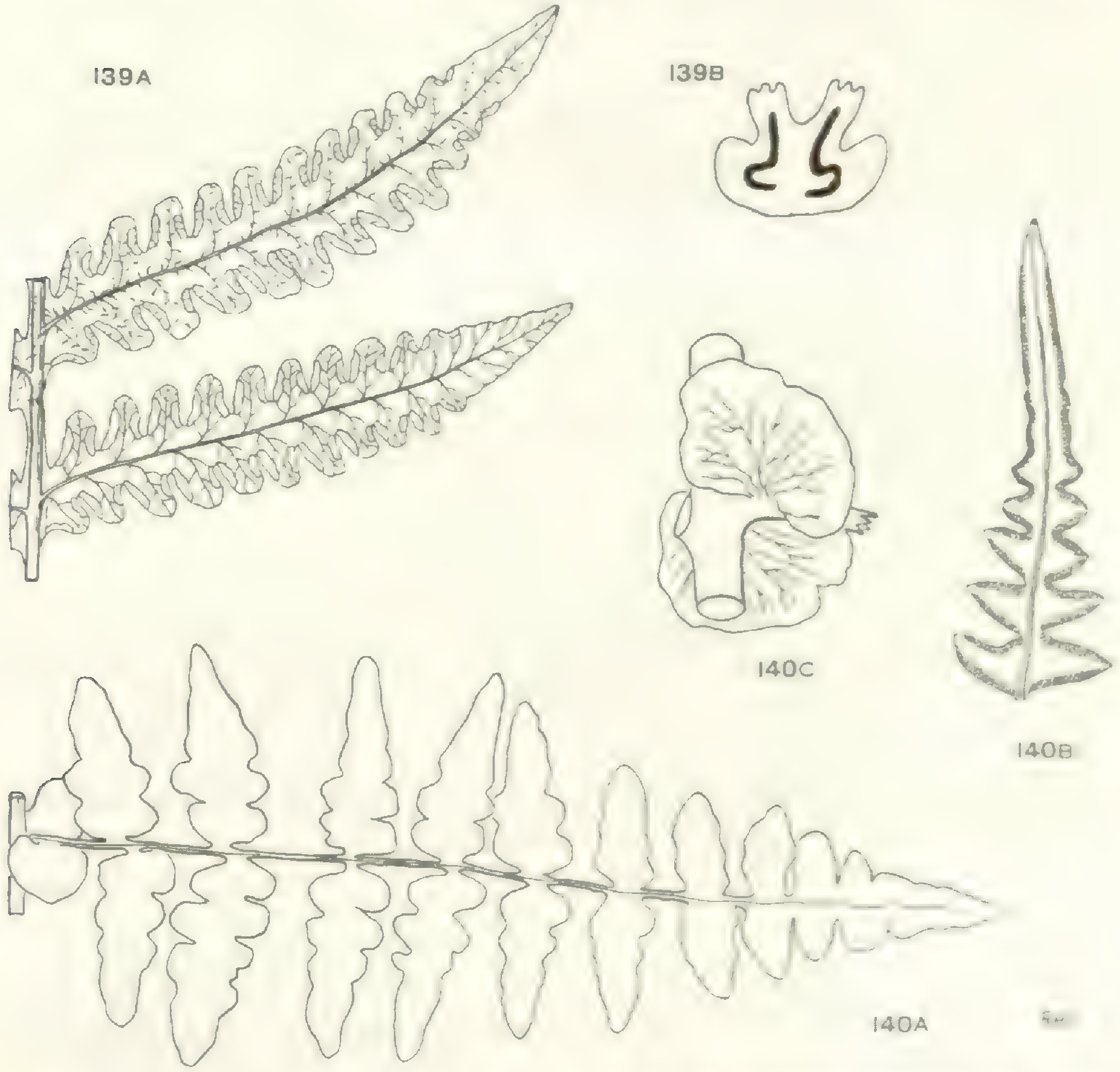
24. HISTIOPTERIS (Ag.) J. Sm. Hist. Fil. 294. 1875.

Pteris sect. *Histiopteris* Ag. Rec. Gen. Pterid. 76. 1839. Type: *Pteris vespertilionis* Labill. = *Histiopteris vespertilionis* (Labill.) J. Sm.

Terrestrial, the rhizome slender, long-creeping, scaly and sometimes also pubescent, bearing the leaves at intervals; leaves small to very large, bipinnate-pinnatifid to tripinnate-pinnatifid, glabrate, veins free to anastomosing; sporangia borne on a marginal commissure connecting the vein-tips, covered by an indusium which is formed from the reflexed, modified margin, paraphyses present. — 1 species in America.

Histiopteris incisa (Thunb.) J. Sm. Hist. Fil. 295. 1875. FIG. 140.
Pteris incisa Thunb. Prod. Fl. Cap. 171. 1800. Type: Cap. Bon. Spei, 1774, *Thunberg;* isotype: S-PA!

Rhizome scales brown, mostly long-triangular, more or less clathrate, trichomes, when present, brownish, long and rather soft; leaves ca. 0.5-3 m. (or more) long, petiole short to long, scaly toward or at the base with scales similar to those on the rhizome, lamina ovate-triangular to long-triangular, pinnae opposite, the basal pinnules reduced, especially toward the base of the lamina of large leaves, where they become stipule-like, pinnules often opposite, glaucous beneath and glabrous or with scattered, brownish, large trichomes; indusium membranous, glabrous, entire to crenulate.



FIGS. 139-140. Fig. 139. *Lonchitis hirsuta:* A, fertile pinnules, indument and venation, × ¾, Venezuela, *Fendler 100*, GH; B, petiole section, × 2, Honduras, *Steeres & Ray 385* GH. Fig. 140. *Histiopteris incisa:* A, sterile, pinna, × ½, Colombia, *Killip & Smith 20209*, GH; B, apex of fertile segment, × ½, Bolivia, *Steinbach 8961*, GH; C, stipular pinnules at base of a lower pinna, × 1, *idem.*

The venation is unusually variable in this species. Most commonly it is partially areolate; less often it is almost wholly areolate and rather rarely it is wholly open, all of the veins being free.

Tropical America; Old World.

Shrubby slopes and dense forest, Huánuco to Puno, 1000-3000 m.

Specimens seen: HUANUCO: Carpish, *Sandeman 5193* (K); Panao, *Macbride 3603* (F, US). JUNIN: Huacapistana, *Weberbauer 2194* (B); Villa Amoreti, *G. Kunkel 637* (GH); San Nicolás, Pichis Trail, *Killip & Smith 25961* (US). CUZCO: Valle de Pillahuata, Paucartambo, *Herrera 3337, 3341* (US). PUNO: Sandia, *Weberbauer 714* (B); between Sandia and Río Chunchusmayo, *Weberbauer 1341* (B).

25. PTERIS L. Sp. Pl. 2: 1073. 1753; Gen. Pl. 484. 1754. Type: *Pteris longifolia* L. The typification of the genus has been discussed by Maxon (Jour. Bot. 61: 7. 1923).

Terrestrial, the rhizome usually stout, scaly, erect and bearing the leaves in a crown or cluster, to long-creeping and bearing the leaves at intervals; leaves of medium size to large or very large, 1-pinnate to 5-pinnate, glabrous to pubescent or sparingly scaly, veins free or anastomosing; sporangia borne on a marginal commissure connecting the vein-tips, covered by an indusium which is formed from the reflexed, modified margin, paraphyses present. — About 50 species in South America.

Maxon, W. R. Pteridophyta (Pteris), *in* Sci. Surv. Porto Rico & V. I. 6: 432-436. 1926.

The genus *Pteris* is notable for the manner in which the leaves, especially their basal pinnae, are branched. The extent of the branching may change on the same plant from the small leaves to the largest ones. The type of branching is difficult to use as much as its importance probably warrants, because it is often insufficiently known. Most herbarium specimens consist either of small leaves or of fragments of large leaves. Another unusual feature in *Pteris* is that many species have awns on the upper side of the costa of the penultimate segments. In these species there is a ridge on each side of the costa which is interrupted at each costule and is prolonged into a free awn.

The species predominantly grow in forests or in more open, shrubby or rocky habitats on the eastern slopes and valleys of the Andes. One species, *P. coriacea,* grows in the

Andes proper, and a few others also grow in the Amazon basin. *Pteris vittata* and *P. critica* are local escapes from cultivation.

KEY TO THE SPECIES

a. Veins free (rare areolae may be present). .... b.

b. All pinnae, or those above the base, entire. .... c.

c. Lamina 1-pinnate, pinnae 10 to many pairs, cordate to subcordate, the basal ones reduced. .... 1. *Pteris vittata*

c. Lamina with the basal pinnae usually with a single (rarely more) large pinnule, rarely entire, pinnae one to five pairs, cuneate or decurrent, the basal largest or nearly so. .... 2. *Pteris cretica*

b. All pinnae pinnatifid or more complex (rarely reduced apical ones entire). .... d.

d. Basal pinnae 1-pinnate (or more) beyond the basal pinnules, the pinnules stalked or sessile (constricted at least on the acroscopic side); penultimate segments mostly with the basal inferior segment reduced, or at least shorter than the superior. .. e.

e. Penultimate segments 1-pinnate, except sometimes toward the apex; ultimate segments narrowed at the base, at least on the acroscopic side. .... f.

f. Basal pinnae the largest but each much smaller than the remaining portion of the lamina, ultimate segments entire. .... 3. *Pteris coriacea*

f. Lamina tripartite, ultimate segments, or many of them, lobed. .... 4. *Pteris Bakeri*

e. Penultimate segments deeply pinnatifid, or 1-pinnate only at the base; ultimate segments broadest at the base. .... g.

g. Costa of the penultimate segments shortly muricate to muricate-spiculate beneath (the other axes usually similar), with a deciduous scale (rarely a trichome) borne at the apex of each process; segments coriaceous. .... 5. *Pteris muricata*

g. Costa of the penultimate segments (and other axes) smooth beneath, with deciduous trichomes (rarely scales); segments herbaceous to herbaceous-coriaceous. .... 6. *Pteris deflexa*

d. Basal pinnae deeply pinnatifid to subpinnatisect beyond the one (rarely two or none) basal, enlarged, inferior, pinnatifid pinnule, the ultimate segments fully adnate or laterally joined; penultimate segments mostly with the basal superior segment reduced, or at least shorter than the inferior, or both basal segments reduced. .... h.

h. Veins arising from the costules of the ultimate segments, or near their base; pinnae, except the basal pair, not or hardly reduced at the base or with only the basal superior segment reduced. .... 7. *Pteris quadriaurita*

h. One or two veins, especially in the basal portion of the penultimate segment, arising from the costa of the penultimate segment about half way between adjacent costules; pinnae, except the basal pair, with both basal segments reduced to about half or less the length of the longest. .... 8. *Pteris pungens*

a. Venation areolate, or predominantly so, or at least a row of areolae along the costa of the penultimate segments. .... i.

i. Ultimate segments (usually pinnae or pinnules) stalked, entire, usually large (mostly 15-40 cm. long). .... j.

j. Lamina 1-pinnate (rarely the basal pinnae each with a large pinnule); costal areolae long, with the long axis divergent from the costa, those toward the margin progressively shorter; pinnae minutely tortuous-pubescent beneath, especially on the veins, to glabrate, the sterile margins entire. .... 9. *Pteris grandifolia*

j. Lamina bipinnate toward or at the base, or rarely tripinnate; costal areolae short and broad, those toward the margin longer, those at the margin shorter; pinnae and pinnules minutely straight appressed-pubescent beneath, to glabrate, the sterile margins serrate. .... 10. *Pteris Haenkeana*

i. Ultimate segments joined or sessile, or lobed, often small (5-10 cm. or less long). .... k.

k. Veins free except for a single row of areolae along the costa of the penultimate segments (rarely a few others). .... 11. *Pteris biaurita*

k. Venation predominantly areolate. .... l.

l. Upper side of the costa of the penultimate segments awned at the base of the costules; basal pinnae pinnate-pinnatifid to bipinnate beyond the basal pinnules (except in no. 16 where they are only pinnatifid or are pinnatifid beyond the single enlarged, basal, inferior pinnatifid pinnule). .... m.

m. Two or more areolae, with their long axis parallel to the costa of the penultimate segments, between adjacent costules. .... 12. *Pteris altissima*

m. A single areola, with its long axis parallel to the costa of the penultimate segment, between adjacent costules. .... n.

n. Base of the penultimate segments narrowly decurrent on their stalk, or on the next axis; ultimate segments sharply serrate apically. .... 13. *Pteris propinqua*

n. Base of the penultimate segments abrupt to cuneate, not decurrent (apical ones may be sessile). .... o.

o. Separate portion of the longer ultimate segments about 1½ to 2½, rarely 3, times as long as broad; ultimate segments minutely puberulent to hirsute beneath, sharply serrate apically. .... 14. *Pteris podophylla*

o. Separate portion of the longer ultimate segments about 4 to 6, rarely 3½ to 10 times as long as broad; ultimate segments minutely appressed pubescent beneath to glabrate. .... p.

p. Penultimate segments with an abrupt base, not at all cuneate or decurrent and, all but the apical ones, subpinnatisect to 1-pinnate at the base with at least the basal segments slightly narrowed toward their base; ultimate segments serrate-crenulate to bluntly serrate apically. .... 15. *Pteris livida*

p. Penultimate segments cuneate at the base, pinnatipartite, with the basal segments broadest at their base; ultimate segments entire to sharply serrate apically. .... q.

q. Areolae converging on the sinus of the ultimate segments few and broad; the vein that forms the long, costal areola arising from the costule or near to it. .... 16. *P. reticulatovenosa*

q. Areolae converging on the sinus of the ultimate segments numerous and very narrow; the vein that forms the long, costal areola arising from the costa well beyond the costule that is basal to it. .... 17. *P. speciosa*

l. Upper side of the costa of the penultimate segments not awned; basal pinnae entire to pinnatifid beyond the single enlarged, basal, inferior pinnule. .... r.

r. Pinnae entire or irregularly lobed. .... 19. *Pteris petiolulata*

r. Pinnae regularly lobed or pinnatifid. .... s.

s. Penultimate segments hirsute on both surfaces and on the margin and especially so on the costae. .... 18. *Pteris Lechleri*

s. Penultimate segments glabrous to minutely pubescent. .... t.

t. Lobes or ultimate segments sharply serrate at the apex; pinnae lobed to shallowly or moderately pinnatifid. .... 17. *Pteris speciosa*

t. Ultimate segments bluntly serrate at the apex; pinnae (except the basal pair) deeply pinnatifid. .... 20. *Pteris horizontalis*

1. **Pteris vittata** L. Sp. Pl. 2: 1074. 1753. Type: China, *Osbeck*, LINN 1246.3, photo A. FIG. 141.

Rhizome stout, short-creeping, the leaves forming a rosette in small plants, a cluster in large ones, leaves 5-150 cm. (or more) long, the petiole much shorter than the lamina; lamina 1-pinnate, narrowed to the base, pinnae at least 10 pairs in small leaves to usually numerous, the sterile margins serrate, short-petiolulate, the base cordate to subcordate, glabrous or nearly so beneath except for the moderately to sparingly pubescent costa, veins free.

This species is very distinct from the other Peruvian ones. In the past it has been confused with *Pteris longifolia*

(Mexico, West Indies to Brazil) but that species has articulate pinnae, the petiolule being abruptly attached to the rachis and somewhat enlarged, while in *P. vittata* the petiolule is evenly and somewhat decurrently joined to the rachis.

A species of the Old World, often cultivated and sometimes becoming naturalized in tropical and subtropical America.

Sea cliffs near Lima and on banks of the Río Rímac, Lima, sea level to ca 1500 m.

Specimens seen: LIMA: north of Chorillos, *Stork 9367* (GH, UC); Santa Eulalia, *Coronado 2* (GH, UC, US); Chosica, *Soukup 2047* (F, US); Miraflores, *Tryon & Tryon 5217* (BM, F, GH, U, UC, US, USM); km. 75, Carretera Central, *Saunders 371* (BM).

2. **Pteris cretica** L. Mant. 130. 1767. Type: Crete, LINN 1246.7, photo A. FIG. 142.

Rhizome small to moderately stout, short-creeping, leaves 15-100 cm. (or more) long, the petiole usually longer than the lamina, the fertile leaves taller than the sterile; lamina 1-pinnate to usually bipinnate at the base (rarely above), broadest at the base or nearly so, pinnae 1-5 pairs, the basal with a large, inferior pinnule which rarely is branched, (rarely with more pinnules, or the second pair of pinnae with pinnules), simple pinnae and pinnules petiolulate to sessile, the base cuneate or decurrent, the sterile margins entire to usually serrulate or serrate, glabrous or nearly so beneath or sometimes slightly pubescent or also scaly on the costa, veins free.

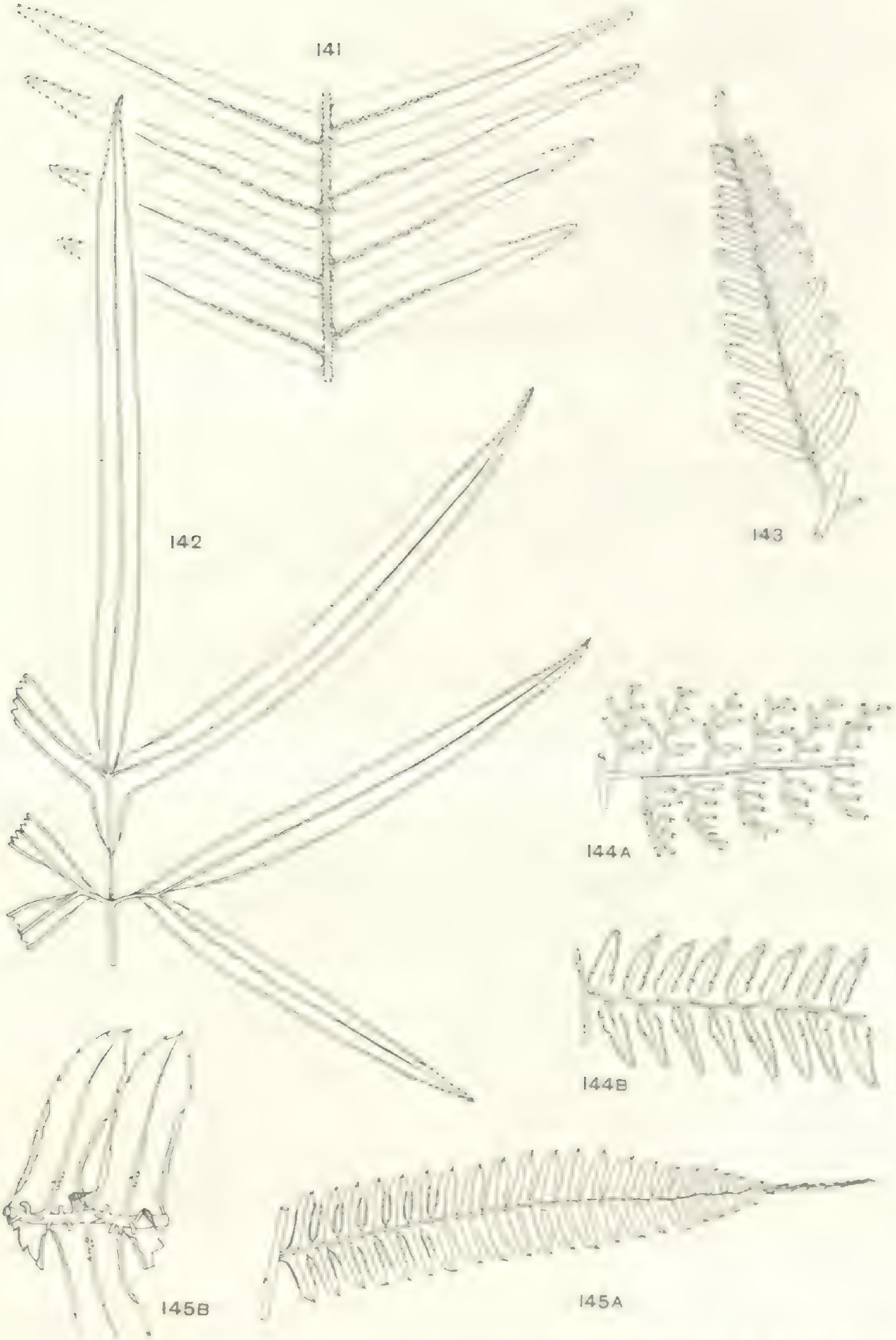
A native of the Old World and perhaps of Mexico; cultivated in Peru and probably sometimes becoming naturalized.

Specimens seen: AMAZONAS: Poma Cocha, *Steere* (GH). LIMA: Botanical Garden of Lima, 1954, *Coronado 189* (UC).

3. **Pteris coriacea** Desv. Mém. Soc. Linn. Paris 6: 300. 1827. Type: Peru, *Dombey*, P! photo GH. The sheet in Herb. Desvaux is marked as the type, it contains a sterile leaf of this species and a portion of a fertile leaf of *Pteris muricata;* the sheet in Herb. Gen. P! contains a fertile and sterile leaf of this species. FIG. 143.

Pteris Jamesonii Hook. Sp. Fil. 2: 193, t. 133A. 1858. Lectotype: Quito, Ecuador, *Jameson*, K!

Rhizome moderately stout, short-creeping, leaves 30-70 cm. (or more) long, the petiole about as long as the lamina, or longer; lamina bipinnate to tripinnate at the base, the basal pinnae largest, pinnae short- to definitely petiolulate, with the basal inferior pinnule usually shorter than the superior (except on the basal ones), the costa unawned above or very bluntly awned, smooth to muricate-spiculate beneath; ultimate



FIGS. 141-145. Fig. 141. *Pteris vittata:* portion of sterile lamina, × ¾, Peru, *Tryon & Tryon 5217*, GH. Fig. 142. *P. cretica:* fertile lamina, × ½, Mexico, *Ghiesbreght 262*, GH. Fig. 143. *P. coriacea:* sterile pinna, × ½, Peru, *Dombey*, P. Fig. 144. *P. Bakeri:* A, base of sterile pinna, × ¾, Peru, *Pearce*, K; B, base of fertile pinna, × ½, *idem*. Fig. 145. *P. muricata:* A, fertile penultimate segment, × ⅓, Colombia, *Killip & Smith 16594*, GH; B, ultimate segments and axis, lower surface, × 2, Ecuador, *Rimbach 166*, GH.

segments narrowed at the base on both sides or at least on the acroscopic side, the sterile margins entire to serrate, glabrous beneath except for the deciduously scaly costa, veins free.

This species differs from *P. muricata* principally in its 1-pinnate rather than pinnatisect penultimate segments, and it is perhaps not wholly distinct. It is a rare species and has been frequently confused with the more common *P. muricata.*

Ecuador and Peru.

Crevices of shaded rocks and canyon walls, Ancash to Apurímac, 2800-3500 m.

Specimens seen: ANCASH: cerca a Llamac, prov. Bolognesi, *Cerrate 2372* (GH, USM). HUANUCO: Chasqui, *Macbride & Featherstone 1755* (F, US). LIMA: between San Mateo and Parac, *Coronado 312* (GH, UC). JUNIN: Tarma, *G. Kunkel 406* (GH). APURIMAC: Ampay, *Vargas 1062* (GH, US).

4. **Pteris Bakeri** C. Chr. Ind. Fil. 593. 1906, based on *P. decomposita* Baker, Syn. Fil. ed. 2, 479. 1874, not Gaud. 1827. Type: Muña, Peru, *Pearce*, K! fragment NY! FIG. 144.

Rhizome evidently rather slender and long-creeping but perhaps stout and short-creeping in large plants, leaves 0.5 to perhaps 2 m. long, the petiole about as long as the lamina; lamina broadly triangular, tripartite, each of the basal pinnae almost as large as the upper portion, quadripinnate at the base, bipinnate to tripinnate above the basal pinnae, pinnae petiolulate, penultimate segments with the basal inferior pinnule usually shorter than the superior, their axes bluntly to definitely awned above, deciduously scaly and long muricate-spiculate beneath; ultimate segments usually lobed, often deeply so, cuneate at the sessile base, glabrous beneath or slightly scaly on the costa, veins free.

The tripartite lamina and the sessile, usually lobed, ultimate segments are evidently sufficiently distinctive characters of this species. However, the scanty material available does not allow a proper assessment of it.

Peru.

Forest, Huánuco and Junín, ca. 2800 m.

Specimens seen: HUANUCO: Muña, *Pearce*, (K); Pozuzo, *Pearce 534* (K). JUNIN: Carpapata, above Huacapistana, *Killip & Smith 24488* (US).

5. **Pteris muricata** Hook. Sp. Fil. 2: 193, t. 123B. 1858. Type: Antioquia, Colombia, *Jervise*, K! FIG. 145, MAP 39.

Rhizome short- to long-creeping, ascending to decumbent, leaves 0.5 to 2 m. (or more) long, the petiole about as long as the lamina, or longer; lamina bipinnate to tripinnate at the base, tripartite or nearly so, usually 1-pinnate above the basal pinnae which are the largest and regularly 1-pinnate or with a single, enlarged, basal, inferior, 1-pinnate pinnule, penultimate segments pinnatisect or subpinnatisect (rarely 1-pinnate at the base), short-petiolulate to subsessile, the basal inferior segment usually shorter than the superior, the costa bluntly to definitely awned above, deciduously scaly (rarely also pubescent) and shortly muricate to muricate-spiculate beneath; ultimate segments mostly as broad at the base as above, or broader, the sterile margins entire to strongly serrate, glabrous beneath except for the slightly scaly or pubescent costule, veins free.

I am not certain of the validity of maintaining this species distinct from *P. coriacea*, or from the next one, *P. deflexa*. It differs from *P. coriacea* in its pinnatisect penultimate segments, although in some cases they are 1-pinnate at the base. It differs from *P. deflexa* in the firmer texture of the leaf and in its muricate, rather than smooth, costae which bear scales. However, sometimes the costae are only slightly muricate and rarely they may bear trichomes, as in *P. deflexa*.

Specimens of this species have often been identified as *P. coriacea*, perhaps because Hooker (Sp. Fil. 2: t. 124) confused the two; his plate of *P. coriacea* is *P. muricata*.

Mexico to Colombia and Bolivia.

Forests and among moist rocks, Huánuco to Puno, 1700-2400 m.

Selected specimens: HUANUCO: Mito, *Macbride & Featherstone 1619* (F, US); Huacachi, near Muña, *Macbride 4167* (F, US). PASCO: Quillesú, *Soukup 3283* (GH). JUNIN: Huacapistana, *Killip & Smith 24191* (US); Pariahuanca, *Mathews 1295* (K); Carpapata, *G. Kunkel 619* (GH). APURIMAC: Chirhuai, *Vargas 2302* (US); arriba de Abancay, *Ferreyra 9808* (GH, USM). CUZCO: Machu-Picchu, *Tryon & Tryon 5398* (BM, F, GH); Tres Cruces, prov. Paucartambo, *Vargas 1055* (GH, US). PUNO: between Ayapata and Kahualluyoc, prov. Carabaya, *Vargas 10751* (GH); Tabina, *Lechler 2030* (B, K).

6. **Pteris deflexa** Link, Hort. Berol. 2: 30. 1833. Type: Brazil, *Hort. Bot. Berol.* B! photo GH. FIG. 146.

Pteris polita Link, Hort. Berol. 2: 30. 1833. Type: Brazil, *Hort. Bot. Berol.* B! photo GH.

Rhizome moderately to very stout (6-8 cm. in diameter), short-creeping or ascending, leaves 0.5-3 m. long, the petiole about as long as the lamina, or longer; lamina bipinnate to tripinnate at the base, 1-

pinnate to bipinnate above the basal pinnae which are the largest and may have one or two enlarged, basal, inferior, 1-pinnate pinnules, penultimate segments pinnatipartite to usually pinnatisect, petiolulate to subsessile, the basal inferior segment usually shorter than the superior, the costa awned above, smooth beneath and deciduously pubescent (rarely with scales); ultimate segments as broad at the base as above, or broader, the sterile margins sharply to coarsely serrate, glabrous beneath or the costule slightly pubescent or scaly, veins free.

This species is close to the previous one, *P. muricata*, and the differences are discussed under that species.

Greater Antilles; South America.

In dense forest, San Martín to Ayacucho, 800-1800 m.

Specimens seen: SAN MARTIN: Tarapoto, *Spruce 4326* (BM, GH, K, US). LORETO: Sinchono, prov. Coronel Portillo, *Aguilar 898* (GH, USM). JUNIN: La Merced, *Soukup 1028* (F), *Killip & Smith 23902* (US); Huacapistana, *Ferreyra 503* (GH, USM); Chanchamayo valley, *Schunke 1* (F), *1386* (F, US). AYACUCHO: Ccarrapa, between Huanta and Río Apurímac, *Killip & Smith 22408* (F, GH, US).

7. **Pteris quadriaurita** Retz. Observ. Bot. 6: 38. 1791. Type: Ceylon, *König*. FIG. 147.

Pteris edentula Kze. Linnaea 9: 75. 1834, as *Pteris biaurita* var. ? *P. edentula*. Type: Pampayacu, Peru, *Poeppig 223 (Diar. 1106)*; isotype: B! photo GH.

Rhizome moderately stout, erect or decumbent, leaves about 0.5-2 m. long, the petiole about as long as the lamina, or longer; lamina bipinnate at the base, 1-pinnate above the basal or lower pinnae, the basal pinnae about the same length as those above, each with an enlarged, basal, inferior, pinnatifid pinnule, (rarely with a second such pinnule, or the second and third pairs of pinnae with such a pinnule), penultimate segments petiolulate to subsessile, the costa awned above and glabrous or slightly pubescent beneath, pinnatipartite to pinnatisect, the basal inferior segment usually longer than the superior; ultimate segments as broad at the base as above, or broader, entire, glabrous or slightly and usually minutely pubescent beneath, mostly on the costule, veins free.

The suggestion of T. G. Walker (Evolution 12: 91. 1958) "... that the name *P. quadriaurita* should not in future be used in any sense other than that of Retzius *sens. strict.* ..." (for the plant of southern India and Ceylon) is based on a cytological study but can hardly be accepted as a taxonomic judgment.

Tropical America; Old World.

Dense forests, woods and thickets, in soil or in rocky places, Lambayeque to Cuzco, 700-2200 m.

Selected specimens: LAMBAYEQUE: km. 32 on road from Olmos to Jaén, *Correll & Smith P830* (GH). HUANUCO: Río Huallaga, below Río Santo Domingo, *Macbride 4233* (F, US); Pampayacu, *Macbride 5048* (F, US). JUNIN: La Merced, *Killip & Smith 23473, 23686* (F, US), *Cerrate 2832* (GH, USM), *Soukup 3409* (US); Huacapistana, *Aguilar 508* (GH, USM). CUZCO: Potrero, *Tryon & Tryon 5367* (BM, F, GH, U, US, USM), *Vargas 8236* (UC); Río Lucumayo, Urubamba valley, *Sandeman 3546* (K).

8. **Pteris pungens** Willd. Sp. Pl. 5: 387. 1810. Type: Hispaniola. FIG. 148.

Rhizome moderately stout, erect, or decumbent, leaves about 0.5-2 m. long, the petiole about as long as the lamina, or longer; lamina bipinnate at the base, 1-pinnate above the basal pinnae which are about as long as those above and have a single enlarged, basal, inferior, pinnatipartite pinnule, penultimate segments petiolulate to subsessile, the costa awned above and glabrous or nearly so beneath, pinnatipartite, the basal segments reduced; ultimate segments as broad at the base as above, or broader, the sterile margins entire to serrate, glabrous beneath or nearly so, veins free.

Pteris pungens is rather similar to the previous species, *P. quadriaurita*, from which it differs especially in the veins that arise from the costa about half way between adjacent costules (that is, more or less beneath the sinus). These occur particularly toward the base of the penultimate segment. In *P. quadriaurita* all of the veins arise from the costules or very near to them. Also, both basal segments of the penultimate segments are reduced in *P. pungens* while in *P. quadriaurita* only the superior one is reduced.

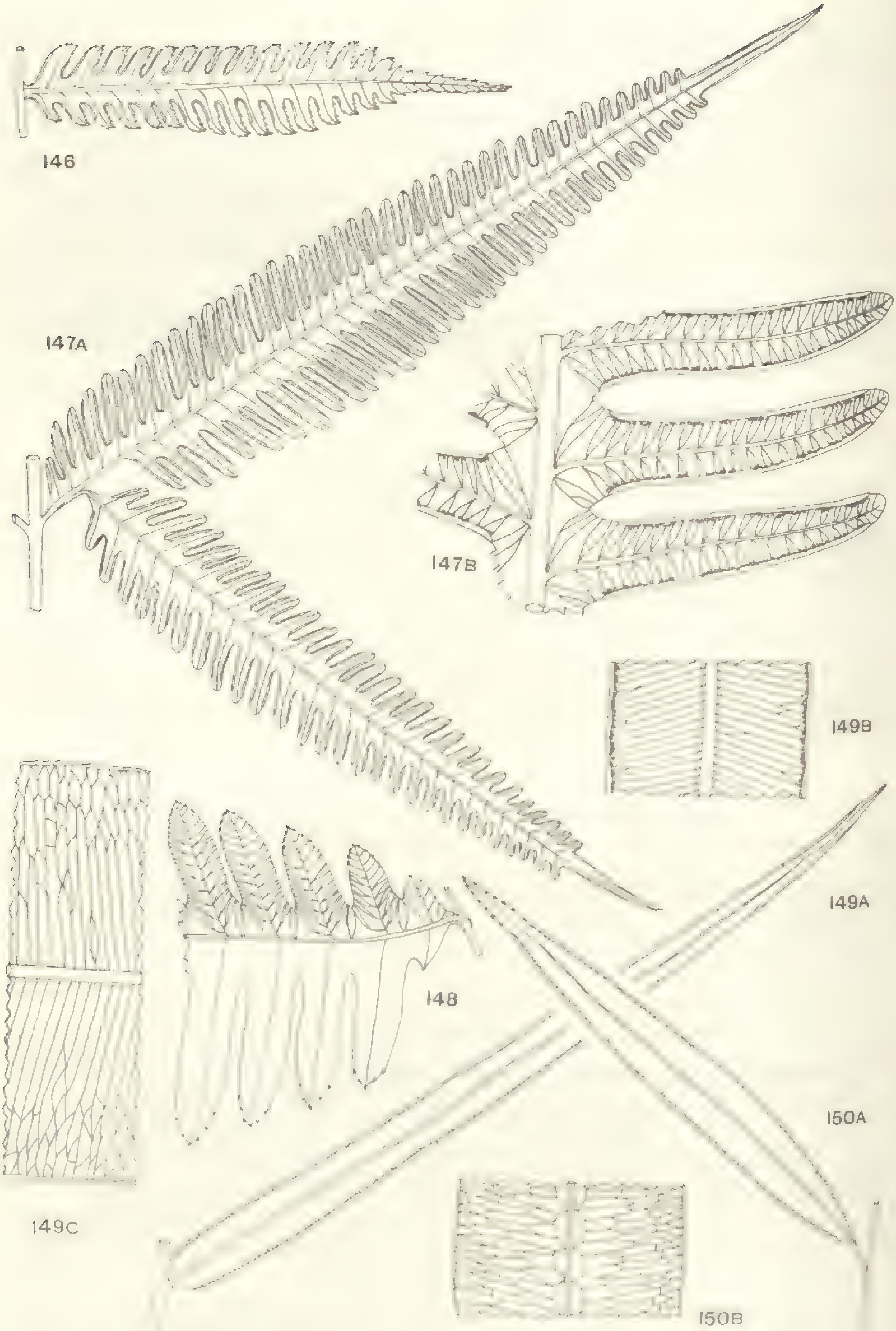
Mexico to Panama; West Indies; British Guiana to Colombia, south to Bolivia.

Specimens seen: SAN MARTIN: Tarapoto, *Spruce 4750* (K), *Woytkowski 35215* (UC). LORETO: Yurimaguas, *L. Williams 3865* (F, US), *Killip & Smith 28012* (US); Balsapuerto, *Killip & Smith 28517* (GH, US). HUANUCO: Ganzo Azul, Río Pachitea, *Sandeman 3361* (K).

9. **Pteris grandifolia** L. Sp. Pl. 2: 1073. 1753. Type: Dominica or Martinique, LINN 1246.1, photo A. FIG. 149, MAP 40.

Pteris grandifolia var. *campanae* Rosenst. Fedde Rep. Spec. Nov. 7: 291. 1909. Type: Tarapoto, (monte Campana) Peru, *Spruce 4668*: isotype: K!

Rhizome about 1 cm. in diameter, rather extensively creeping, leaves



Figs. 146-150. Fig. 146. *Pteris deflexa:* fertile penultimate segment, × ½, Colombia, *Killip & Smith 18973*, GH. Fig. 147. *P. quadriaurita:* A, fertile basal pinna, × ½, Ecuador, *Camp E3309*, GH; B, fertile ultimate segments, × 1½, Mexico, *Pringle 3971*, GH. Fig. 148. *P. pungens:* base of pinna, × ¾, Bolivia, *R. S. Williams 1185*, GH. Fig. 149. *P. grandifolia:* A, fertile pinna, × ¼, Colombia, *Killip 9730*, GH; B, portion of fertile pinna, × 1, *idem;* C, portion of sterile pinna, × 1, Peru, *Tryon & Tryon 5287*, GH. Fig. 150. *P. Haenkeana:* A, fertile pinna, × ¼, Colombia, *Killip & Smith 16510*, GH; B, portion of sterile pinna, × 1, *idem.*

1-5 m. long, the petiole about as long as the lamina, or longer; lamina 1-pinnate (rarely bipinnate at the base with each basal pinna with an enlarged, basal, inferior, entire pinnule), the lower pinnae somewhat shorter than those above, pinnae simple entire, (except rarely the basal), long- to short-petiolulate, minutely tortuous-pubescent beneath, especially on the veins, to glabrate; venation areolate, the costal areolae long, with their long axis divergent from the costa, those toward the margin progressively shorter.

Small portions of a leaf may be distinguished from the next species, *P. Haenkeana*, by the pattern of the venation mentioned in the key and by the entire, rather than serrate, sterile margins.

West Indies; Mexico to Peru.

In forest or more commonly, thickets, forest borders, and along stream banks, Amazonas to Junín, 135-1100 m.

Selected specimens: AMAZONAS: entre Aramango y Montenegro, prov. Bagua, *López et al. 4214* (GH). SAN MARTIN: Chazuta, Río Huallaga, *Klug 4013* (F, GH, K, UC); Tarapoto, *Spruce 4668* (K), *4751* (BM, K). LORETO: Río Marañon, above Pongo de Manseriche, *Mexia 6182* (F, GH, K, UC, US); Puerto Arturo, Yurimaguas, *L. Williams 5109, 5348* (F), *Killip & Smith 27852* (US). HUANUCO: Tingo María, *Tryon & Tryon 5287* (BM, F, GH, U, US, USM); Puente Durand, 1945, *Vargas* (GH, USM). PASCO: Oxapampa, *Soukup 2349* (F, GH). JUNIN: Puente Perené, *Coronado 277* (UC); La Merced, *Killip & Smith 23693* (F, GH, US), *Cerrate 2825* (GH, USM).

10. **Pteris Haenkeana** Presl, Rel. Haenk. 1: 55. 1825. Type: *Haenke*, PR; authentic specimen: Colombia, *Linden 1028*, W! det. Presl. FIG. 150, MAP 41.

Pteris ampla Kze. Linnaea 9: 74. 1834. Type: Pampayacu, Peru, 1829, *Poeppig (Diar. 1154)*; isotype: K!

Rhizome about 1 cm. in diameter, extensively creeping, leaves 1-2 m. long, the petiole about as long as the lamina, or longer; lamina fully bipinnate at or toward the base or rarely tripinnate, the basal pinnae the largest, pinnae and pinnules short- to usually long-petiolulate minutely straight appressed-pubescent beneath to glabrate, the sterile margins sharply serrate; venation areolate, the costal areolae short and broad, those toward the margin longer, those at the margin shorter.

The differences between *P. Haenkeana* and the previous species, *P. grandifolia*, are discussed under that species. It is closely related to, if not conspecific with, *Pteris mexicana* of Mexico and Central America.

Colombia to Bolivia and Brazil.

MAPS 39-42. Map 39, *Pteris muricata*. Map 40, *P. grandifolia*. Map 41, *P. Haenkeana*. Map 42, *P. altissima*.

In forests, San Martín, to Cuzco, 600-1400 m.

Specimens seen: SAN MARTIN: Juan Jui, *Klug 4256* (F, GH, K, UC, US); Zepelacio, near Moyobamba, *Klug 3492* (F, GH, K, US); Tambo María, *Stübel 1108* (B). HUANUCO: Pampayacu, *Kanehira 147* (GH, US), *Poeppig 1154* (K); Cushi, *Bryan 724* (F, GH, US). JUNIN: La Merced, *Soukup 1091* (F); San Ramón, *Schunke A178* (US); Vitoc, *Ruiz 38* (B); Perené, *G. Kunkel 505* (GH); Chanchamayo valley, *Schunke 27, 70* (F). AYACUCHO: Aina, between Huanta and Río Apurímac, *Killip & Smith 22717* (F, GH, US). CUZCO: Ccochayoc, *Büés 1726* (US).

11. **Pteris biaurita** L. Sp. Pl. 2: 1076. 1753. Type: Martinique, Jamaica or Hispaniola, LINN 1246.19, photo A. FIG. 151.

Rhizome moderately stout, erect to decumbent, leaves about 0.6-1 m. long, the petiole about as long as the lamina, or longer; lamina bipinnate at the base, 1-pinnate above the basal pinnae which are about the same length as those above and have a single enlarged, basal, inferior, pinnatifid pinnule, pinnae petiolulate to sessile, the costa awned above and glabrous or minutely appressed-pubescent beneath, deeply pinnatifid (except for the pinnule on the basal pinnae), with the basal inferior segment usually longer than the superior; ultimate segments broadest at the base, glabrous or minutely appressed-pubescent beneath, the sterile margins entire to subcrenulate, veins free except for a single costal areola between adjacent costules, or occasionally a few other basal veins joined.

The venation is characteristic of this species and easily separates it from the others in Peru. Small sterile leaves (the lamina less than 10 cm. long) have the basal pinnae with the enlarged pinnule typical of adult leaves but the remainder of the lamina is only pinnatifid.

Mexico to Panama; West Indies; Guianas to Colombia to Peru and Brazil; Old World.

In forest, in clearings and along forest borders, Loreto to Cuzco, 400-1500 m.

Specimens seen: LORETO: Boquerón Padre Abad, *Allard 22115* (US). HUANUCO: Pozuzo, *Macbride 4596* (F); Tingo María, *Tryon & Tryon 5246* (GH, U, US). JUNIN: Satipo, *Ridoutt* (US); San Ramón, *Schunke A180* (US); Río Paucartambo, near Perené Bridge, *Killip & Smith 25277* (F, US); Chanchamayo valley, *Schunke 24, 1001* (F). CUZCO: Chacanares, prov. Convención, *Vargas 13680* (GH).

12. **Pteris altissima** Poir. Lam. Encycl. 5: 722. 1804. Type: Porto Rico, *Ledru* (Herb. Lamarck) P! photo GH. FIG. 152, MAP 42.

Pteris elata Ag. Rec. Gen. Pterid. 63. 1839. Type: Panama, *Cuming 1267*, K!; isotype: GH!

Pteris Kunzeana Ag. Rec. Gen. Pterid. 62. 1839. Syntypes: Peru, *Mathews 1802*, K! fragment NY!; Peru, *Poeppig 225*, B! photo GH. (Two other specimens cited, not seen).

Rhizome erect in young plants, becoming short- to rather long-creeping, leaves 0.8-2.5 m. long, the petiole about as long as the lamina, or longer; lamina bipinnate, the basal pinnae much the largest, pinnae petiolulate to subsessile, penultimate segments with the costa awned above and glabrous or minutely appressed-pubescent beneath, moderately pinnatifid to pinnatisect, with the basal inferior segment shorter than the superior, or not; ultimate segments broadest at the base, minutely appressed-pubescent beneath, the sterile margin entire to sharply serrate, venation areolate, two or more costal areolae with their long axis parallel to the costa, between adjacent costules.

Pteris altissima is a variable species, especially in characters of the texture, shape and disposition of the ultimate segments. I believe that *Pteris sclerophylla* Sod. and *P. esmeraldense* Sod. are synonyms but I have not seen authentic material of them.

The leaves of young plants have the lamina more complex in relation to their size, than leaves of old plants. Small leaves are bipinnate with narrow segments, older leaves on the same plant are progressively less complex and have broader segments.

Mexico to Panama; West Indies; Guianas to Colombia, south to Bolivia; Brazil.

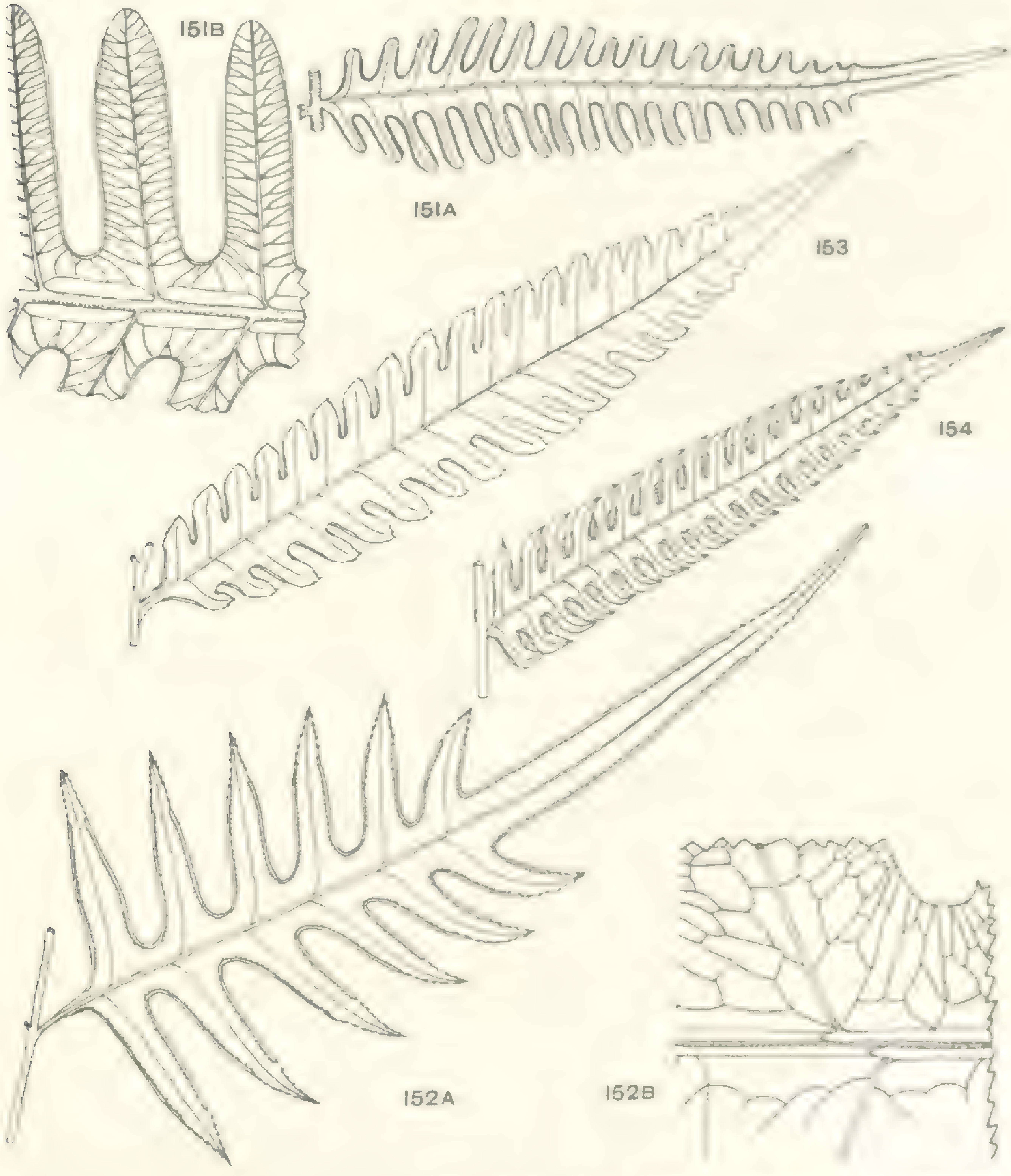
In woods and forests, Amazonas to Cuzco, 100-1500 m.

Selected specimens: AMAZONAS: Río Utcubamba, 40 km. s. of Bagua Grande, *Hutchison 1486* (GH). SAN MARTIN: Tarapoto, *Spruce 4061* (BM, K); Zepelacio, near Moyobamba, *Klug 3704* (F, GH, K, US). LORETO: mouth of Río Santiago, above Pongo de Manseriche, *Mexia 6125* (F, GH, K, UC, US), *6125a* (GH, K, UC, US); Iquitos, *Killip & Smith 27440* (US). HUANUCO: Tingo María, *Tryon & Tryon 5229* (BM, F, GH, U, USM); Pampayacu, *Kanehira 150* (GH, US). JUNIN: La Merced, *Soukup 1098* (F), *Killip & Smith 23684* (US). AYACUCHO: near Kimpitiriki, Río Apurímac valley, *Killip & Smith 23039* (US). CUZCO: Cosñipata, *Vargas 11260* (GH); Quincemil, *Vargas 11725* (GH).

13. **Pteris propinqua** Ag. Rec. Gen. Pterid. 65. 1839. Lectotype: Jamaica, *Bancroft*, K! FIG. 153.

Rhizome moderately stout to stout, erect, leaves 0.5-1.5 m. long, the petiole about as long as the lamina, or longer; lamina bipinnate, the basal pinnae the largest, pinnae petiolulate to subsessile, penultimate segments with the costa awned above and glabrous or minutely appressed-pubescent beneath, deeply pinnatifid to pinnatipartite, with the basal inferior segment shorter than the superior, or not, the base narrowly decurrent on its stalk or onto the next axis; ultimate segments minutely appressed-pubescent beneath, the sterile margins serrate to sharply serrate, venation areolate, with one costal areola with its long axis parallel to the costa, between adjacent costules.

Among the species with areolate veins, *P. propinqua* is distinctive in having the base of the penultimate segments decurrent on the stalk, or onto the next axis.



Figs. 151-154. Fig. 151. *Pteris biaurita:* A, fertile pinna, × ½, Mexico, *Langlassé 707*, GH; B, portion of fertile pinna, × 1½, Peru, *Tryon & Tryon 5246*, GH. Fig. 152. *P. altissima:* A, fertile pinna, × ½, Costa Rica, *Dodge & Thomas 6421*, GH; B, portion of pinna, upper surface, awns on pinna-rachis, × 2½, Peru, *Tryon & Tryon 5229*, GH. Fig. 153. *P. propinqua:* fertile pinna, × ¾, Colombia, *Haught 3772*, GH. Fig. 154. *P. podophylla:* fertile pinna, × ½, Colombia, *Pennell et al. 8610*, GH.

Mexico to Panama; Jamaica; Colombia to Bolivia and Brazil.

Forests, Loreto, Huánuco and Junín, 100-700 m.

Specimens seen: LORETO: Río Itaya, *Killip & Smith 29620* (US); Gamitanicocha, Río Mazán, *Schunke 282* (F, GH, UC, US); Paraiso, upper Río Itaya, *L. Williams 3356* (F, US); Puerto Arturo, *Killip & Smith 27895* (US), *L. Williams 5253* (F). HUANUCO: Tingo María, *Allard 21920* (US). JUNIN: Puerto Bermudez, *Killip & Smith 26639* (US).

14. **Pteris podophylla** Sw. Jour. Bot. Schrad. 1800(2):67. 1801, based on *Lonchitis pedata* L. Sp. Pl. ed. 2, 2: 1536. 1763, not *Pteris pedata* L. Type: Jamaica, *P. Browne*, LINN 1249.1; Browne, Nat. Hist. Jam. t. 1, f. 1, 2. FIG. 154.

Pteris trialata Sod. Crypt. Vasc. Quit. 107. 1893. Type: Nieblí, Ecuador, *Sodiro;* isotype: P! photo GH.

Rhizome very stout, evidently creeping; leaves 0.75-2 m. (or more) long, the petiole about as long as the lamina; lamina 3- to 5-pinnate and subpalmately branched at the base, the basal pinnae much the largest, pinnae long-petiolulate to sessile, penultimate segments sessile or short-stalked with the costa awned above and pubescent to glabrate beneath, shallowly pinnatifid to pinnatipartite, the base not decurrent, the basal inferior segment usually shorter than the superior, or not; ultimate segments minutely puberulent to hirsute beneath, venation areolate, one long areola with its long axis parallel to the costa, between adjacent costules.

Pteris podophylla is a rather variable species, especially in the size of the ultimate segments and the degree to which they are pubescent. The nearly palmate type of branching of the lamina is distinctive, although rarely represented in speciments.

Mexico to Panama; Greater Antilles; Colombia to Bolivia.

Forests, San Martín to Cuzco, 1000-1800 m.

Selected specimens: SAN MARTIN: Zepelacio, near Moyobamba, *Klug 3495* (F, GH, K, US). LORETO: Sinchona, cerca a Divisoria, prov. Coronel Portillo, *Aguilar 844* (GH, USM). HUANUCO: Carpish, *Sandeman 5203* (K), *Ferreyra 1831* (GH, USM), *2123* (BM); Tingo María, *Ridoutt* (GH, USM). PASCO: Oxapampa, *Soukup 2344* (F, GH). JUNIN: San Ramón, *Killip & Smith 24686* (F, US); Chanchamayo, *Schunke 149* (US), *743, 966* (F). CUZCO: San Miguel, *Cook & Gilbert 1114* (US); Valle de Pillahuata, *Herrera 1609* (US).

15. **Pteris livida** Mett. Ann. Sci. Nat. V, 2: 222. 1864. Lectotype: Choachi, Bogotá, Colombia, *Lindig 179*, B! photo GH; isotype: BM! GH! P! US! FIG. 155.

Pteris Andreana Sod. Crypt. Vasc. Quit. 102. 1893. Type: Ecuador, *Sodiro;* isotype: **P!; authentic specimens: GH! NY! US!**

Rhizome evidently stout, creeping, leaves 2-6 m. long, the petiole about as long as the lamina; lamina bi- to tripinnate at the base, mostly 1- to bipinnate above the basal pinnae which are much the largest, pinnae short- to long-petiolulate, penultimate segments with the costa awned above and minutely pubescent to glabrate beneath, pinnatipartite to pinnatisect, or 1-pinnate at the base, the base abrupt (not cuneate or decurrent), the basal inferior segments about the same length as the superior; ultimate segments minutely appressed-pubescent beneath, especially on the veins, the basal ones (and sometimes others) narrowed toward their base, the sterile margins entire to serrate-crenulate, venation areolate, one long costal areola with its long axis parallel to the costa, between adjacent costules.

Most of the Peruvian material of *P. livida* has been identified as *Pteris gigantea* Willd. That species, however, has two areolae, with their long axis parallel to the costa, between adjacent costules and it also differs in characters of the arrangement and shape of the segments.

Costa Rica to Panama, Colombia to Bolivia.

Forests, Loreto and Huánuco, 1500-2400 m.

Specimens seen: *Poeppig 186* (P). LORETO: Cerro de Escaler (between Yurimaguas and Moyabamba), *Ule 6885* (B). HUANUCO: Muña, *Macbride 4322* (F, US); Hacienda Mercedes, Prov. Huánuco, dist. Churubamba, *Mexia 8219* (F, GH, K, UC, US); Pampayacu, *Kanehira 150bis* (GH, US), *Poeppig* (B); Mirador, prov. Huánuco, 1940, *Ridoutt* **(GH, USM); Cochero,** ***Dombey 53*** **(P).**

16. **Pteris reticulatovenosa** Hieron. Hedwigia 48: 243. 1909, based on *P. reticulata* Kuhn, Linnaea 36: 91. 1869, not Desv. 1811. Lectotype: **Peru,** ***Pavon,*** **B! photo GH.** **FIG. 156.**

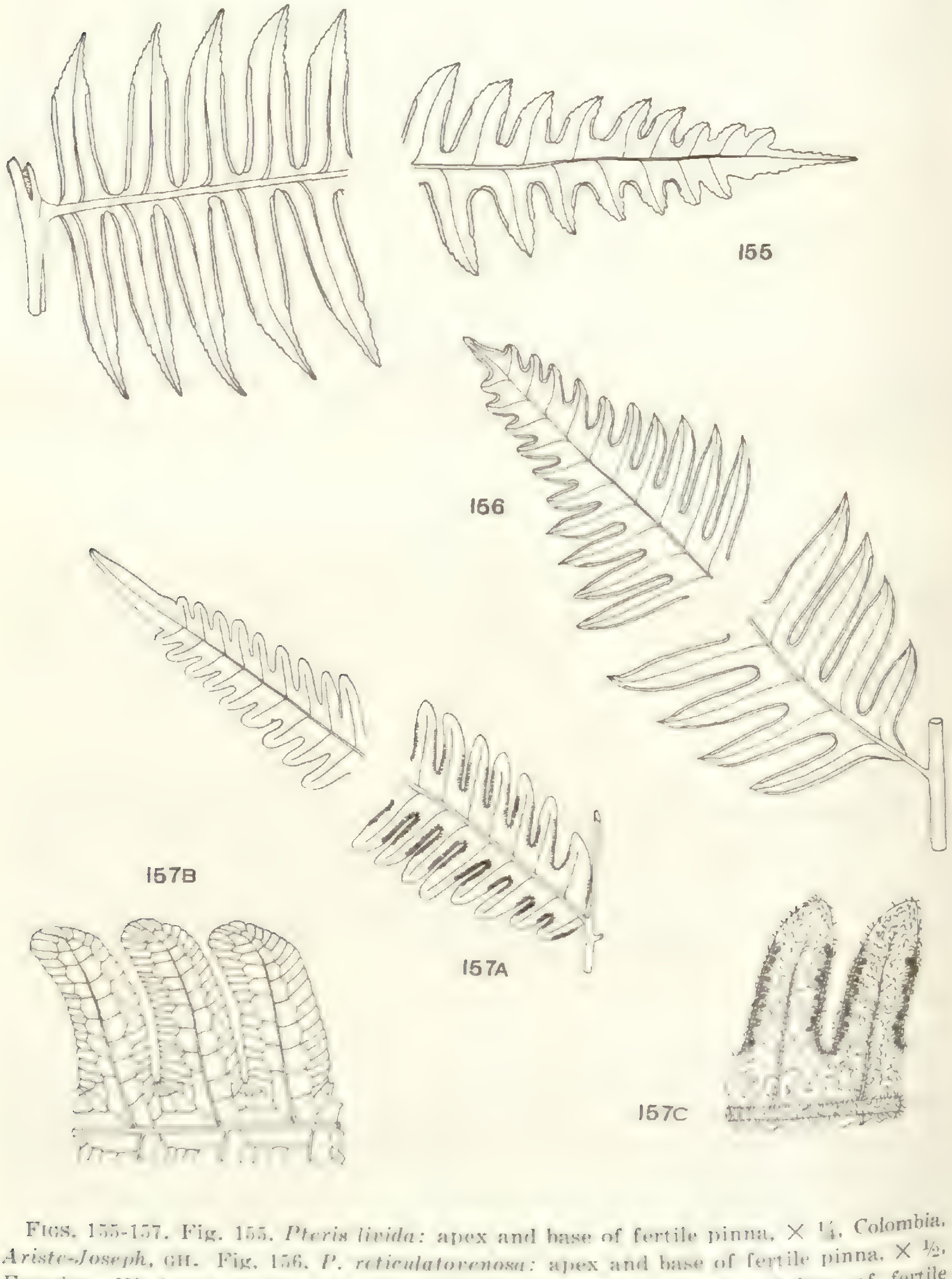
Pteris nuda Copel. Univ. Cal. Publ. Bot. 19: 302. 1941. Type: Huánu-**co, Peru,** ***Mexia 8299,*** **UC!; isotype: GH!**

Rhizome stout, evidently decumbent, leaves about 1-2 m. long, the petiole about as long as the lamina; lamina 1-pinnate, or bipinnate at the base and each basal pinna with an enlarged, basal, inferior, pinnatipartite pinnule, the basal pinnae about as long as those above, pinnae petiolulate to subsessile, the costa awned above and glabrous or minutely appressed-pubescent beneath, pinnatipartite (except the basal when a pinnule is present), with the basal inferior segment usually longer than the superior, the base cuneate; ultimate segments broadest at the base, the sterile margin entire to serrulate, minutely appressed-pubescent beneath, venation areolate, with a single costal areola, with its long axis parallel to the costa, between adjacent costules.

This species and the next one, *P. speciosa,* are rather closely related; the characters of their venation which may serve to identify them are mentioned in the key.

Colombia to Peru.

In forests and on wooded, rocky slopes, San Martín to Cuzco, 600-1700 m.



FIGS. 155-157. Fig. 155. *Pteris livida:* apex and base of fertile pinna, × ¼, Colombia, *Ariste-Joseph,* GH. Fig. 156. *P. reticulatovenosa:* apex and base of fertile pinna, × ½, Ecuador, *Hitchcock 21838,* GH. Fig. 157. *P. Lechleri:* A, apex and base of fertile pinna, × ½, Peru, *Klug 3680,* GH; B, portion of sterile pinna, venation, × 1½, Peru, *Killip & Smith 23962,* GH; C, portion of fertile pinna, indument, × 1½, Peru, *Klug 3680,* GH.

Specimens seen: *Pavon* (B); *Ruiz 40* (B). SAN MARTIN: Tarapoto, *Spruce 4752* (B, K). HUANUCO: Pozuzo, *Macbride 4718* (F, US); Riachuela Chontalagua, *Mexia 8299* (GH, K, UC). JUNIN: La Merced, *Soukup 1031* (F); Dos de Mayo, Pichis Trail, *Killip & Smith 25812* (US); Chanchamayo, 1909, *Schunke* (BM). CUZCO: entre Quincemil y San Lorenzo, *Vargas 11724* (GH).

17. **Pteris speciosa** Kuhn, Linnaea 36: 91. 1869. Lectotype: St. Gavan, (Río San Gaban), Peru, *Lechler 2326*, B! photo GH, fragment NY! US! FIG. 159.

Rhizome not seen, leaves about 0.5-1.0 m. long; lamina 1-pinnate, the basal pinnae about as long as those above, pinnae petiolulate, lobed to moderately pinnatifid, with the basal inferior segment (or lobe) shorter than the superior, the costa unawned or awned above; lobes or ultimate segments broadest at the base, the sterile margins sharply serrate, glabrous or minutely pubescent beneath, venation areolate, a single costal areola, with its long axis parallel to the costa, between adjacent costules.

Pteris speciosa appears to be a distinct species but the material available for study has been so limited that its status remains in some doubt. It is unusual in having the costa either awned or unawned. The characters of venation which separate it from *P. reticulatovenosa* are given in the key.

Colombia to Peru.

In forests, San Martín and Puno, ca. 1000-1500 m.

Specimens seen: SAN MARTIN: Tarapoto, *Spruce 4757* (BM), *4759*, also marked *4757* (K). PUNO: San Gaban (Río), *Lechler 2326* (B, NY, US).

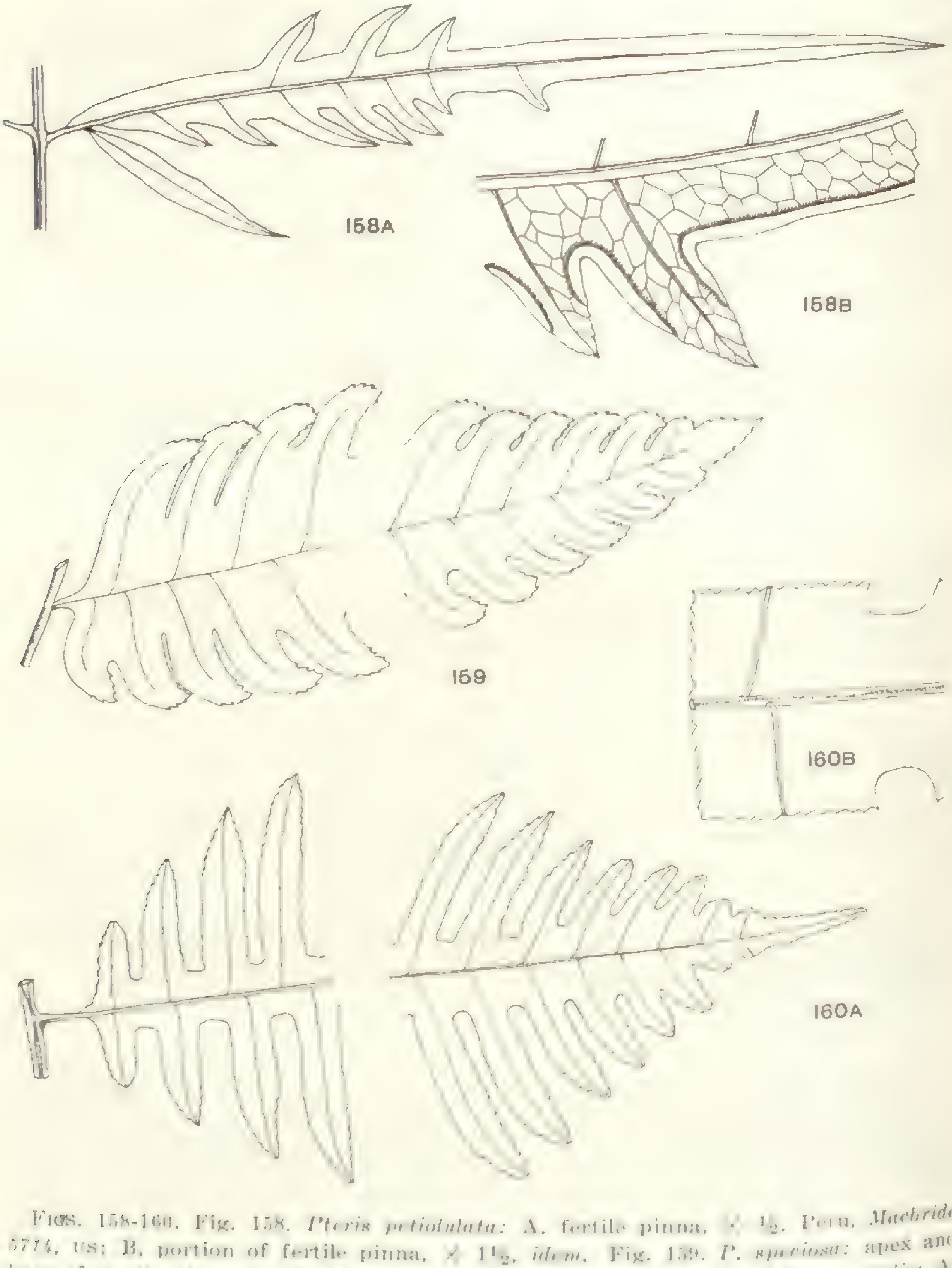
18. **Pteris Lechleri** Mett. Fil. Lechler. 2: 13. 1859. Type: Tatanara (prov. Carabaya, Dept. Puno), Peru, *Lechler 2533*, B! photo GH. FIG. 157.

Pteris vestita Baker, Syn. Fil. 169. 1867. Type: Tarapoto, *Spruce 4063*, K! photo US, fragment US!

Pteris Killipii Maxon, Amer. Fern Jour. 23: 107. 1933, *(nom. superfl., illegit.)*. Type: the same as that of *Pteris vestita*.

Rhizome small to moderately stout, erect, leaves about 0.5-1.25 m. long, the petiole about as long as the lamina, or longer; lamina 1- to bipinnate at the base, 1-pinnate above the basal pinnae which are about as long as those above and have a single enlarged, basal, inferior, moderately to deeply pinnatifid segment or pinnule, pinnae short-petiolulate to sessile, with the costa unawned above and hirsute beneath, moderately pinnatifid to pinnatipartite (except for the basal pair), the basal segments reduced; ultimate segments hirsute on both surfaces and on the margin, sterile margins subentire to crenulate, venation areolate, one costal areola, with its long axis parallel to the costa, between adjacent costules.

The unawned costa and the markedly hirsute segments are distinctive characters of this species. Leaves of young plants (the lamina about 5-9 cm. long) have the basal pinnae pinnatifid and the remainder of the lamina is pinnatifid.



FIGS. 158-160. Fig. 158. *Pteris petiolulata:* A. fertile pinna, × ½, Peru, *Macbride 5714*, US; B. portion of fertile pinna, × 1½, *idem.* Fig. 159. *P. speciosa:* apex and base of sterile pinna, × ½, Colombia, *Daniel 1211*, US. Fig. 160. *P. horizontalis:* A. apex and base of sterile pinna, × ½, Bolivia, *Steinbach 9327*, GH; B. portion of pinna, upper surface, × 1½, *idem.*

Peru and Bolivia.
Forests, San Martín to Puno, 840-1500 m.

Specimens seen: SAN MARTIN: Tarapoto, *Spruce 4063* (K); Zepelacio, near Moyobamba, *Klug 3680* (F, GH, K, US); Lamas, *L. Williams 6400* (F, US). HUANUCO: Tingo María, *Allard 21195, 21201, 21205a, 21594* (US). JUNIN: near La Merced, *Killip & Smith 23919* (US), *23962* (F, GH, US); La Merced, *Macbride 5713* (F, US); San Ramón, *Killip & Smith 24697* (US). CUZCO: Tocate, *Bües 1740* (US). PUNO: Tatanara, prov. Carabaya, *Lechler 2533* (B).

19. **Pteris petiolulata** Tryon, Rhodora 62: 9. 1960. Type: La Merced, Peru, *Macbride 5714*, US!; isotype: F! FIG. 158.

Rhizome rather small, erect, leaves about 0.75-1.5 m. long, the petiole about as long as the lamina; lamina bipinnate at the base, 1-pinnate above the basal or lower pinnae, which are about as long as those above and have a single enlarged, basal, inferior, simple pinnule, pinnae short-petiolulate to sessile, pubescent above and beneath, at least on the costa and costules and sometimes on the margin, entire, or with a basal pinnule, or irregularly and incompletely pinnatifid or lobed mostly on the basiscopic side, the pinnatifid or lobed pinnae with a long entire apex, the costa unawned above, sterile margins entire to serrulate at the tip; venation areolate, several costal areolae between adjacent costules (when present).

This species has been confused with *Pteris Fraseri* of Ecuador from which it differs, most obviously, in the several stalked or sessile pinnae. *Pteris Fraseri* has only the basal pinnae stalked; the lamina above them is pinnatipartite. *Pteris denticulata* of the West Indies to Brazil, Argentina and Bolivia is also related and differs in its serrate-spinescent sterile margins.

Venezuela to Peru.
Forests, Junín and Cuzco, 500-1500 m.

Specimens seen: JUNIN: San Ramón, *Killip & Smith 24696* (F, GH, US); La Merced, *Macbride 5714* (F, US); Chanchamayo, *Schunke 985* (F). CUZCO: Río Pachiri, *Bües 1767* (US).

20. **Pteris horizontalis** (Fée) Rosenst. Meded. Rijks Herb. 19: 10. 1913. FIG. 160.

Litobrochia horizontalis Fée, Crypt. Vasc. Brésil, 1: 48, t. 12, f. 1. 1869. Type: Brazil, *Glaziou 2314*; fragment ex Fée, NY!

Rhizome moderately stout, short-creeping, decumbent, leaves about 1 m. long, the petiole about as long as the lamina; lamina bipinnate at the base, 1-pinnate above the basal pinnae which are about as long as those above and have a single enlarged, basal, inferior, pinnatipartite pinnule, pinnae short-petiolulate to sessile, the upper ones decurrent onto the rachis, the costa unawned above, and glabrous beneath, pinnatipartite, the basal inferior segment longer than the superior, or not; ultimate segments glabrous or minutely appressed-pubescent, the sterile margin subentire to crenulate-serrate; venation areolate, one (or less often two) costal areolae, with their long axis parallel to the costa, between adjacent costules.

The single collection of this species that I have seen from Peru bears no indication of the habitat or altitude.

Peru, Bolivia and Brazil.

Cuzco.

Specimen seen: CUZCO: Valle de Pillhuata, prov. Paucartambo, *Herrera 1621* (US).

26. ACROSTICHUM L. Sp. Pl. 2: 1067. 1753; Gen. Pl. 484. 1754. Type: *Acrostichum aureum* L.

Terrestrial, or palustral, the rhizome very stout, erect, scaly, bearing the leaves in a crown or cluster; leaves very large, 1-pinnate, glabrous to pubescent, veins anastomosing; sporangia borne all over the surface of the fertile pinnae, nearly to the plane, slightly modified margin, indusium absent, paraphyses present. — 2 species in America.

Maxon, W. R. Pteridophyta (Acrostichum), *in* Sci. Surv. Porto Rico & V. I. 6: 401-402. 1926.

This genus has only recently been discovered in Peru (1962) and I did not examine the material until it was too late to have illustrations prepared. However, the genus is a distinctive one and the palustral habitat, the large 1-pinnate leaves with sporangia completely covering the paraphysate fertile pinnae are characters that will readily identify it. The other American species, *A. aureum*, may also be found in Peru and the following key, adapted from Maxon *(op. cit.)*, will serve to distinguish the two:

Fertile lamina with only the upper pinnae fertile, pinnae well spaced, coriaceous, the long axis of the areolae oblique to the costa of the pinna. .... *A. aureum* L.

Fertile lamina with all, or nearly all, of the pinnae fertile, pinnae crowded, chartaceous, the long axis of the areolae nearly at right angles to the costa of the pinna. .... *A. daneaefolium*

Acrostichum daneaefolium Langsd. & Fisch. Ic. Fil. 5, t. 1. 1810. Type: Ins. St. Catharina, Brazil, *Langsdorff*, LE.

Rhizome scales brown, linear, thick and firm; leaves ca. 1.5-3 m. tall, the fertile with few or no sterile pinnae, petiole shorter than the lamina, stout, with large, ligulate, rather soft, fimbriate scales at the base, lamina linear, pinnae usually close, sometimes imbricate, the fertile somewhat smaller than the sterile, entire, chartaceous, with a cartilaginous edge, glabrous to finely pubescent beneath, venation finely areolate, the long axis of the areolae nearly at right angles to the costa.

Tropical America.

Swamp, with Typha and Eichhornia, Tumbes, 20 m.

Specimen seen: TUMBES: Corrales, prov. Tumbes, *López & Sagástegui 4034* (GH).

TRIBE 8. VITTARIEAE.

27. HECISTOPTERIS J. Sm. Lond. Jour. Bot. 1: 193. 1842. Type: *Gymnogramma pumila* Spreng. = *Hecistopteris pumila* (Spreng.) J. Sm.

Epiphytic, the rhizome very small, creeping, scaly, bearing the leaves in a cluster; leaves very small, furcate, glabrous, veins free; sporangia superficial, borne along a portion of the vein, indusium absent, paraphyses present. — An American genus of 1 species.

Hecistopteris pumila (Spreng.) J. Sm. Lond. Jour. Bot. 1: 193. 1842. FIG. 161.

Gymnogramma pumila Spreng. Tent. Suppl. Syst. Veg. 31. 1828. Type: Surinam, *Weigelt;* isotype: B! P!

Rhizome scales brown, linear or sublinear, clathrate, slightly iridescent, leaves ca. 1-2 cm. long, lamina thin, narrowly to rather broadly flabellate, variously dichotomously or subdichotomously branched or toothed, gradually tapering at the base to the petiole, sporangia borne on the distal (but not the apical) portions of the veins.

Tropical America; widespread but not commonly collected.

Epiphyte or on fallen trunks or branches of trees, Huánuco, 625 m.

Specimen seen: HUANUCO: Tingo María, *Allard 20490* (US).

28. VITTARIA J. E. Sm. Mém. Acad. Turin 5: 413. 1793. Type: *Pteris lineata* L. = *Vittaria lineata* (L.) J. E. Sm.   MAP 43.

Epiphytic, the rhizome small, erect or short-creeping, scaly, bearing the leaves in a cluster; leaves small to medium sized, the lamina simple, entire, glabrous, veins anastomosing, forming one series of areolae on each side of the costa; sporangia borne in a continuous, more or less sunken, line along each of the intramarginal commissures, indusium absent, paraphyses present. — 12 species in America.

Benedict, R. C. A revision of the genus Vittaria J. E. Smith. Bull. Torrey Cl. 41: 391-410. 1914.

Tryon, R. Taxonomic fern notes, IV. — Some American vittarioid ferns, Rhodora 66: 110-117. 1964.

The rhizome scales are brown or darker (light brown in *V. latifolia*) and clathrate; usually they are iridescent, especially when the lateral cell walls are heavily sclerotic.

The term *costate* is used in reference to the rhizome scales of Vittaria to describe the dark cell walls that form more or less distinct lines the length of the scale. Scales that are predominantly two cells broad are 1-costate (Fig. 164D), those that are three, four or more cells broad are 2-costate, 3-costate, to many costate, respectively. The spores are sticky and this character is doubtless related to the epiphytic habit of the genus.

The typification and correct application of the names *V. graminifolia*, *V. Moritziana* and *V. Ruiziana* are discussed in my paper cited above.

KEY TO SPECIES

a. Petiole pale, lighter than the green lamina (or if darkened in age or in drying, then concolorous with the brownish lamina); stem dorsiventral. .... b.
  b. Paraphyses slender, tan to light reddish-brown, the apical cell not, or not much, enlarged; spores reniform, monolete. ...... 1. *V. lineata*
  b. Paraphyses stout, reddish-brown to dark reddish-brown, the apical cell enlarged; spores tetrahedral-globose, trilete. .... 2. *V. graminifolia*
a. Petiole dark, usually reddish-brown to atropurpureous, darker than the lamina; stem radial. .... c.
  c. Petiole terete or oval (it may be flattened only at the very base), not alate, hard. .... d.
    d. Rhizome scales 1-costate (sometimes 2-costate at the base), those on the petiole similar but longer; sporangia in deep grooves near the margin. .... 3. *V. stipitata*
    d. Rhizome scales mostly 4- to 7-costate, those on the petiole longer and narrower; sporangia in shallow grooves back from the margin. .... 4. *V. Moritziana*
  c. Petiole flattened and two-angled throughout, wholly or mostly narrowly alate, firm or rather soft, usually irregularly wrinkled or grooved in drying. .... e.
    e. Rhizome scales mostly dark brown to atropurpureous, with sclerotic lateral cell walls and stout, short teeth; lamina usually 15 or more (rarely less than 10) times longer than broad. .... f.

f. Lamina narrowly elliptic to linear-elliptic, often falcate, with a costal ridge on the upper surface from the base to the center or beyond. .... g.

  g. Long axis of the areolae oblique to the costa (a lateral vein reaches the margin above the point where the next one on the same side arises from the costa). .... 5. *V. remota*

  g. Long axis of the areolae parallel to the costa (a lateral vein reaches the margin below the point where the next one on the same side arises from the costa). .... 6. *V. Gardneriana*

f. Lamina narrowly linear (or narrower), rather straight, lacking a costal ridge on the upper surface at the base (one may be somewhat developed beyond the base). .... 7. *V. Ruiziana*

e. Rhizome scales light brown, with slightly sclerotic lateral cell walls, with long, slender cilia; lamina ca. 5 to 8 times longer than broad (above the alate petiole), elliptic; sporangia borne well back from the margin. .... 8. *V. latifolia*

1. **Vittaria lineata** (L.) J. E. Sm. Mém. Acad. Turin 5: 421. 1793. FIG. 162.

Pteris lineata L. Sp. Pl. 2: 1073. 1753. Type: Santo Domingo, Plumier, Fil. t. 143.

Vittaria filiformis Cav. Descr. 270. 1802. Type: Peru, *Née*, MA, photo F, NY, US; seen by C. Chr. (Dansk Bot. Ark. 9(3): 24. 1937) and placed here with some doubt, the type has no rhizome or petiole base.

Rhizome dorsiventral; leaves ca. 10-100 cm. long, pendent, the petiole pale, lighter than the lamina (or in drying concolorous with it) soft and somewhat flattened; lamina very narrow; sporangia in deep grooves back from the margin.

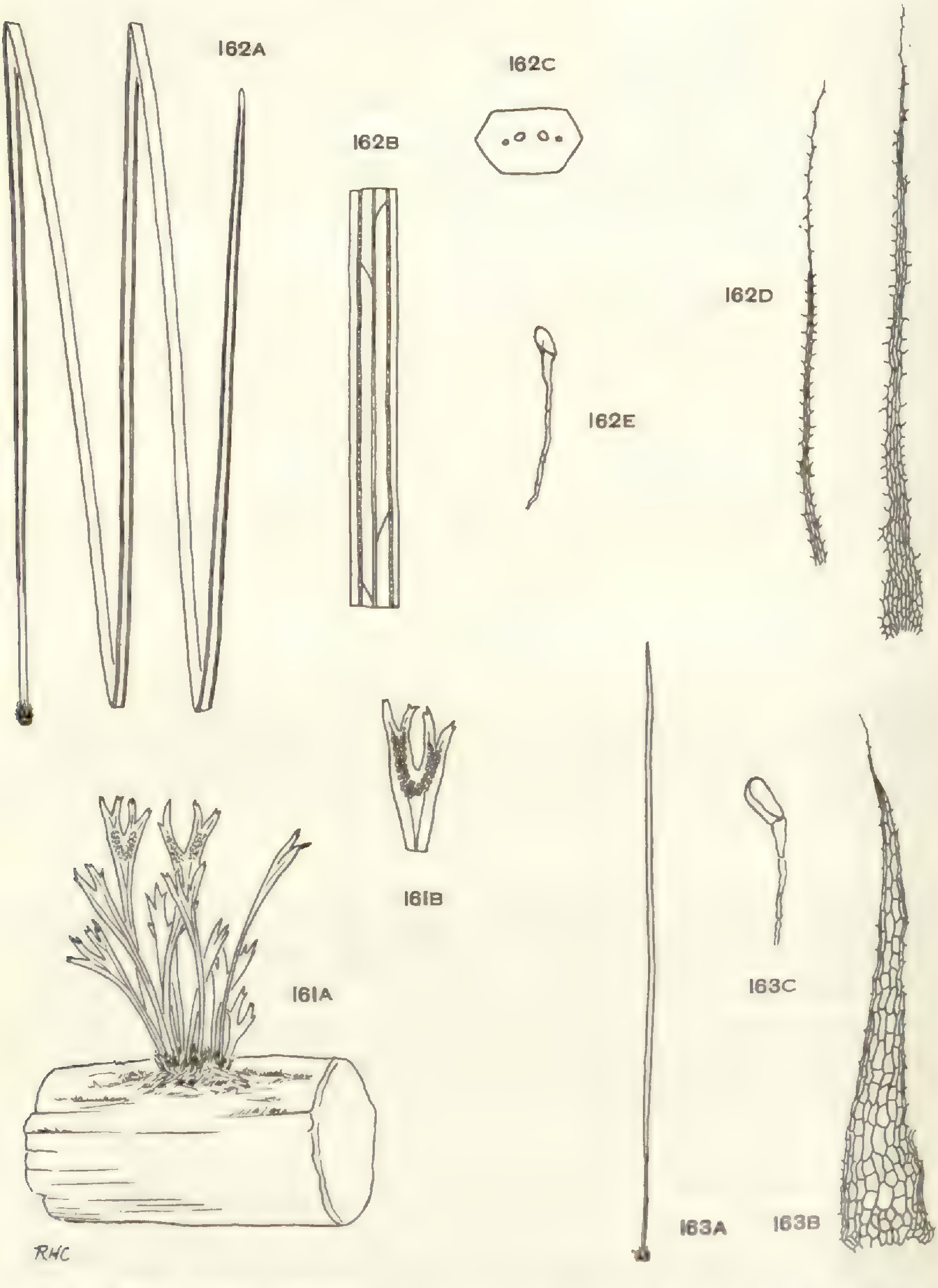
The characters of the spores and of the paraphyses that afford the best characters to distinguish this species from *V. graminifolia* are presented in the key. The following characters, in addition, may be mentioned. The rhizome scales of *V. lineata* usually have a 1-costate, filiform tip and cell walls that are all of the same thickness. In *V. graminifolia*, the rhizome scales usually have a short, 1-costate tip, or none, and the cell walls at the margin of the scale are thinner than those in the center.

I have seen a few specimens (not from Peru) that have the paraphyses of *V. lineata* and the type of spore of *V. graminifolia*, or vice versa.

Tropical America.

Epiphyte in forest, San Martín to Junín, 150-1000 m.

Specimens seen: SAN MARTIN: Tarapoto, *L. Williams 6321* (F, US). LORETO: Santa María, ca. 25 km. below Yurimaguas on Río Huallaga, *Allard 22471* (US). HUANUCO: Tingo María, *Asplund 12356* (US). JUNIN: La Merced, *Weberbauer 1914* (B).



FIGS. 161-163. Fig. 161. *Hecistopteris pumila:* A, plant on twig, × 1, Colombia, *Haught 2080*, GH; B, portion of fertile lamina, × 2, *idem*. Fig. 162. *Vittaria lineata:* A, fertile leaf, × ½, Paraguay, *Fiebrig 5950*, GH; B, portion of fertile lamina, × 1½, *idem;* C, petiole section, × 6, *idem;* D, rhizome scales, × 12, *idem;* E, paraphysis, enlarged, *idem*. Fig. 163. *V. graminifolia:* A, leaf, × ¼, Venezuela, *Pittier 9971*, GH; B, rhizome scale, × 12, *idem;* C, paraphysis, enlarged, *idem*.

2. **Vittaria graminifolia** Kaulf. Enum. Fil. 192. 1824. Isotype: E! (Herb. Greville, Kaulfuss misit 1827, seen in 1964; this must replace my choice of Sello, B, as a lectotype). FIG. 163.

Vittaria filifolia Fée, Mém. Fam. Foug. 3: 20, t. 3, f. 6. 1851-1852. Lectotype: Guadeloupe, *L'Herminier* (Herb. Cosson), P!

Rhizome dorsiventral; leaves ca. 10-50 cm. long, pendent to suberect, the petiole pale, lighter than the lamina (or in drying concolorous with it), soft and somewhat flattened; lamina very narrow; sporangia in deep grooves close to the margin.

The characters of the paraphyses and spores that distinguish this species from the preceding one, *V. lineata*, are presented in the key.

Tropical America.

Epiphyte in forests, Amazonas and Junín, ca. 1200 m.

Specimens seen: AMAZONAS: Tazán, prov. Chachapoyas, *López et al. 4261* (GH). JUNIN: La Merced, *Macbride 5637* (F, US).

3. **Vittaria stipitata** Kze. Linnaea 9: 77. 1834. Type: Pampayacu, Peru, Jul. 1829, *Poeppig (Diar. 1121)*, evidently illustrated in Kze. Anal. Pterid. t. 18, f. 1; isotype: P!; authentic specimen: *Poeppig*, B! photo GH, K! **FIG. 164.**

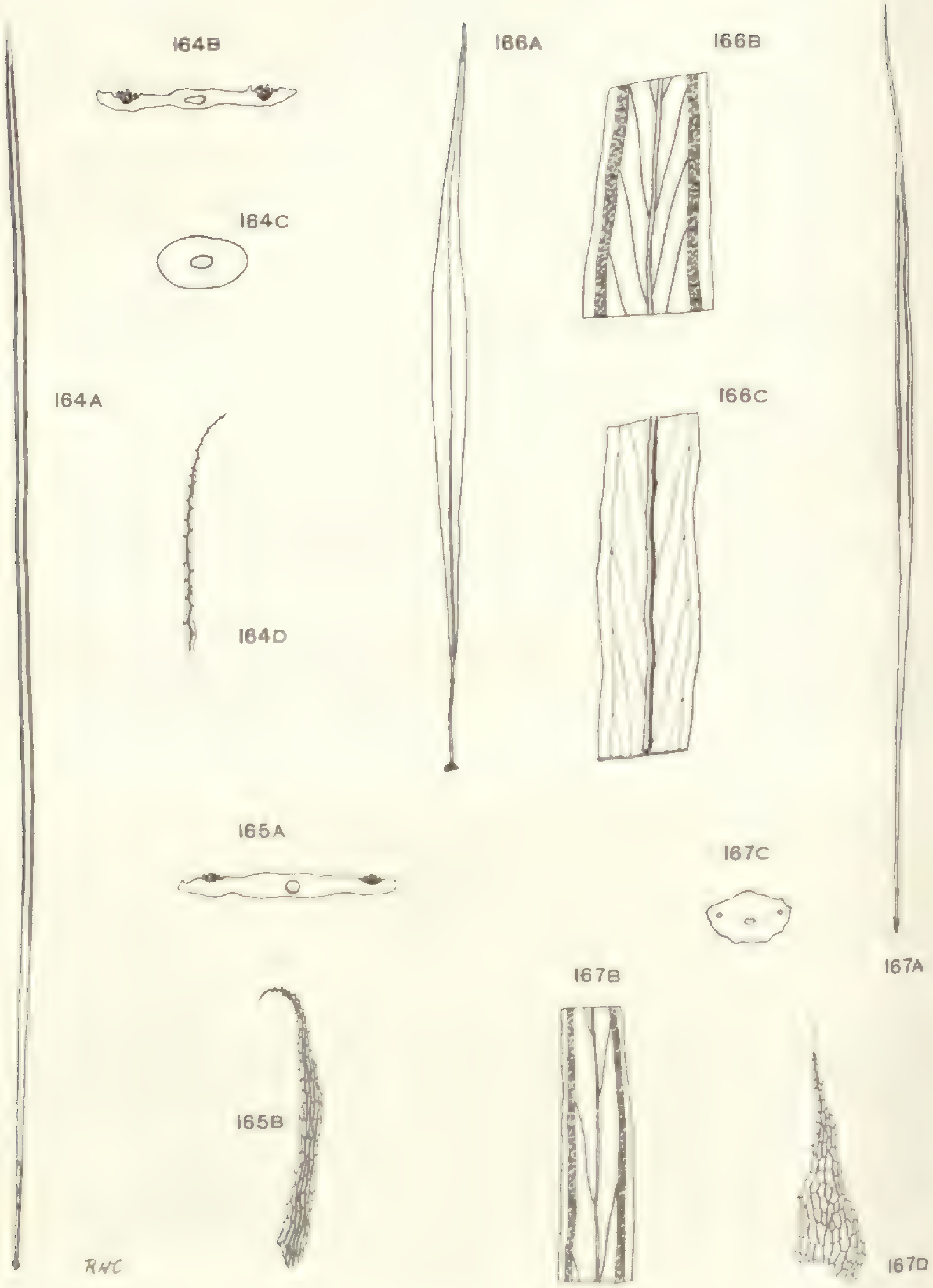
Rhizome radial; leaves ca. 10-75 cm. long, pendent, the petiole dark reddish-brown to atropurpureous, hard, terete or nearly so; lamina narrow; sporangia in deep grooves near the margin.

This species and the next, *V. Moritziana*, are most readily identified by the characters of the sporangial grooves mentioned above and the characters of the rhizome and petiole scales. In *V. stipitata* the rhizome scales are 1-costate or at most 2-costate at their base; in *V. Moritiziana* they are mostly 4- to 7-costate. The petiole scales are similar to those of the rhizome but longer in *V. stipitata*, while in *V. Moritziana* they are also narrower.

Guatemala to Panama; Greater Antilles; Venezuela to Colombia and south to Bolivia; Brazil.

Epiphyte in forests, San Martín to Cuzco, 600-2000 m.

Specimens seen: SAN MARTIN: Cumbassauma Mts., *Steere* (GH); Monte Guayrapurina, prope Tarapoto, *Spruce 4778* (K, P). HUANUCO: Pampayacu, *Poeppig* (B, K, P); Tingo María, *Allard 21932* (US). JUNIN: La Merced, *Soukup 1014* (F). *Macbride 5684* (F, US); above San Ramón, *Killip & Smith 24587* (F, US), *Schunke A117*, *A118* (US); Chanchamayo valley, *Schunke 25* (F), *497* (F, US). CUZCO: Hacienda Idma, prov. Convención, *Weberbauer 5019* (B).



FIGS. 164-167. Fig. 164. *Vittaria stipitata:* A, fertile leaf, × ½, Bolivia, *Steinbach 3759*, GH; B, section of fertile lamina, × 4, *idem*. C, petiole section, × 10, *idem;* D, rhizome scale, × 12, *idem*. Fig. 165. *V. Moritziana*. A, section of fertile lamina, × 3, Colombia, *Pennell 9250*, GH; B, rhizome scale, × 12, *idem*. Fig. 166. *V. remota:* A, leaf, × ¼, Colombia, *Schultes & Villarreal 5242*, GH; B, portion of fertile lamina, lower surface, × 1, *idem;* C, portion of lamina upper surface, × 1, *idem*. Fig. 167. *V. Gardneriana:* A, fertile leaf, × ½, Ecuador, *Camp E3446*, GH; B, portion of fertile lamina, × 1½, *idem;* C, petiole section, × 10, *idem*. D, rhizome scale, × 12, *idem*.

4. **Vittaria Moritziana** Mett. Ann. Sci. Nat. V, 2: 207. 1864. Type: Canoas, Colombia, *Lindig 319*, B! FIG. 165.

Rhizome radial; leaves ca. 10-75 cm. long, pendent, the petiole reddish-brown to atropurpureous, hard, terete or flattened basally, lamina narrow; sporangia in shallow grooves back from the margin.

The characters that best serve to distinguish this species from the preceding, *V. stipitata*, are discussed under that species.

Benedict interpreted this species and name correctly but erroneously applied the earlier name *V. Ruiziana* to it.

Costa Rica and Hispaniola; Venezuela to Colombia, Ecuador and Bolivia; not known from Peru.

5. **Vittaria remota** Fée, Mém. Fam. Foug. 7: 26, t. 20, f. 1, 1857. Type: prov. Ocaña, Colombia, *Schlim 611*. FIG. 166.

Rhizome radial; leaves ca. 5-30 cm. long, erect or suberect, petiole brown to atropurpureous, narrowly alate, flattened, rather soft, wrinkled in drying; lamina narrowly elliptic to elliptic-linear, sometimes subfalcate, with a costal ridge on the upper surface from the base to the center or beyond; sporangia in shallow grooves back from the margin.

This species is rather similar to the next, *V. Gardneriana*, and two can best be distinguished by the characters of the venation mentioned in the key.

Greater Antilles; Surinam to Colombia, Ecuador and Bolivia; not known in Peru.

6. **Vittaria Gardneriana** Fée, Mém. Fam. Foug. 3: 15, t. 3, f. 1, 1851-1852. Lectotype: Brazil, *Gardner 147;* isotype: B! photo GH, BM! K! P! US! FIG. 167.

Rhizome radial; leaves ca. 5-20 cm. long, suberect or pendent, petiole brownish to atropurpureous, narrowly alate, flattened, rather soft, wrinkled in drying; lamina linear-elliptic, often subfalcate, with a costal ridge on the upper surface from the base to the center or beyond; sporangia in shallow grooves back from the margin.

This species is close to the previous one, *V. remota*, and can best be distinguished from it by the characters of venation mentioned in the key.

Costa Rica and Panama; Hispaniola; British Guiana to Colombia, south to Peru; Brazil.

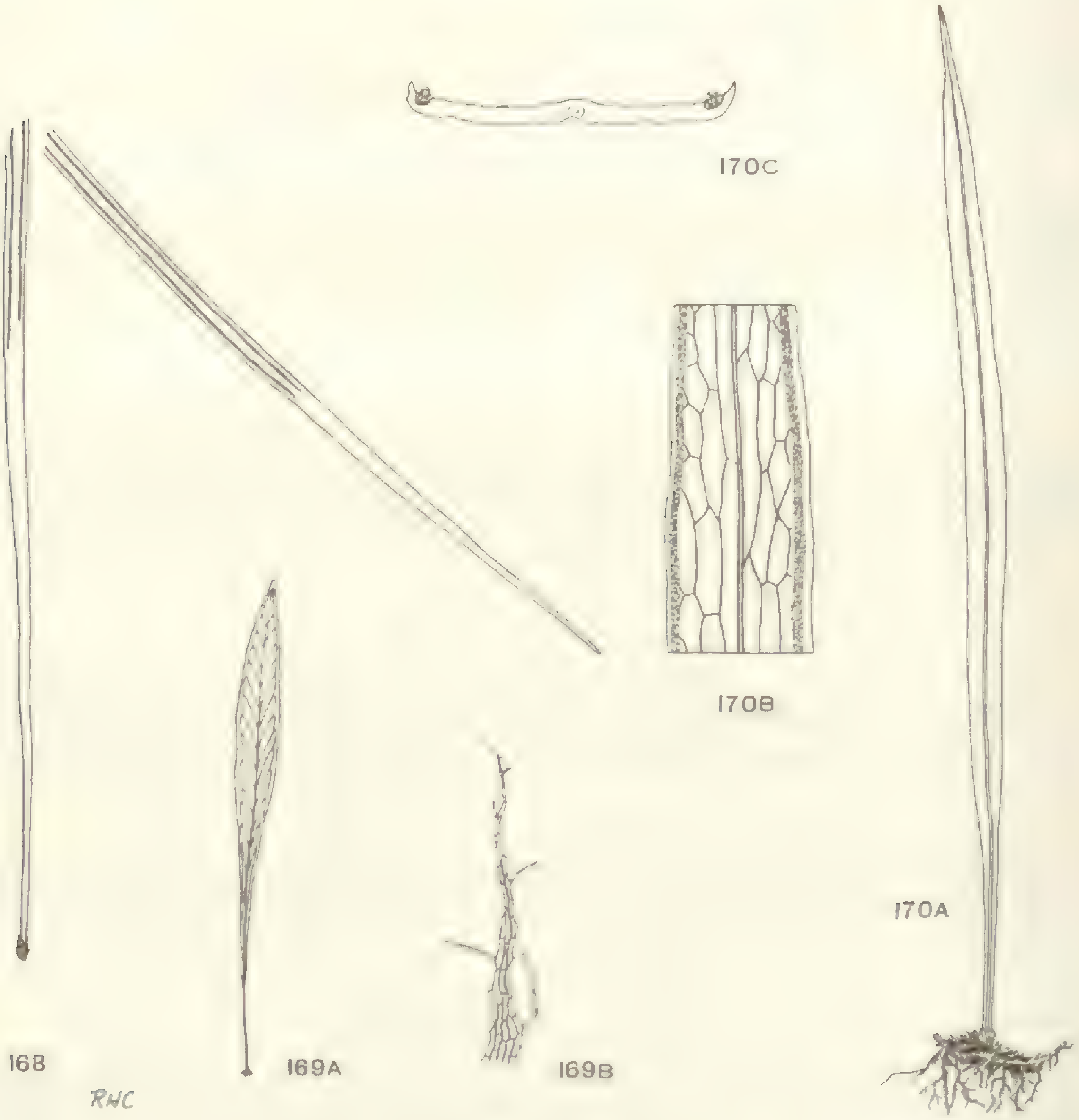
Epiphyte in dense forest, Junín, ca. 1500 m.

Specimens seen: JUNIN: Yapas, Pichis Trail, *Killip & Smith 25552* (F, GH, US).

7. **Vittaria Ruiziana** Fée, Mém. Fam. Foug. 3: 16, t. 3, f. 3. 1851-1852. Type: Peru, *Ruiz;* authentic specimen: Peru, *Dombey* (det. Fée), B! photo GH. FIG. 168.

Pteropsis vittarioides Desv. Mém. Soc. Linn. Paris, 6: 219. 1827. Type: Peru, Herb. Desv., P!, the single leaf evidently taken from Huasi-Huasi, 1779, *Dombey*, P! (a duplicate of this is in Herb. Kunth, B! photo GH).

Vittaria Orbignyana Kuhn, Linnaea 36: 66. 1869. Type: Yungas, Bolivia, *D'Orbigny 229*, B! photo GH; isotype: GH! P! (an excellent specimen), W!



FIGS. 168-170. Fig. 168. *Vittaria Ruiziana:* leaf, × ½, Peru, *Vargas 1588*, GH. Fig. 169. *V. latifolia:* A, leaf, × ¼, Bolivia, *R. S. Williams 1337*, GH; B, rhizome scale, × 12, Peru, *Soukup 2351*, GH. Fig. 170. *Ananthacorus angustifolius:* A, leaf attached to rhizome, × ¼, Bolivia, *R. S. Williams 1345*, GH; B, portion of fertile lamina, × 1, Colombia, *Haught 1649*, GH; C, section of fertile lamina, × 3, *idem.*

Vittaria vittarioides (Desv.) Weath. Contrib. Gray Herb. 114: 34. 1936, not (Thouars) C. Chr. Ind. Fil. 655. 1907.

Rhizome radial; leaves ca. 15-70 cm. long, pendent, petiole dark brown to usually atropurpureous, narrowly alate, flattened, firm, usually grooved in drying; lamina narrow to very narrow, rather straight, lacking a costal ridge on the upper surface at the base, although one may be developed beyond the base; sporangia in rather deep grooves back from the margin.

Venezuela to Colombia, south to Bolivia.
Epiphyte in forest, Huánuco and Cuzco, 1800-3100 m.

Selected specimens: HUANUCO: near Muña, *Macbride 4136* (B, F, GH, US). CUZCO: near Achirani, prov. Paucartambo, *Vargas 1588, 11157* (GH); Cerro Chuyapí, *Bües A44* (GH,US); Valle de San Miguel, *Bües 2187* (US); Huadquiña, *Bües 1344* (US).

8. **Vittaria latifolia** Benedict, Bull. Torrey Cl. 41: 403, t. 17. 1914. Type: Santa Bárbara, Bolivia, *R. S. Williams 1337*, NY!; isotype: GH! US! FIG. 169.

Rhizome radial; leaves ca. 5-18 cm. long, erect ?, petiole dark brown, narrowly alate, flattened, firm, grooved in drying; lamina elliptic, gradually narrowed at the base to the petiole; sporangia in shallow grooves well back from the margin.

The characters of the rhizome scales mentioned in the key are distinctive for this species. Their light brown color corresponds to the only slightly sclerotic cell walls.

Peru and Bolivia.
Pasco.

Specimen seen: PASCO: Oxapampa, *Soukup 2351* (GH).

29. ANANTHACORUS Underw. & Maxon, Contrib. U. S. Nat. Herb. 10: 487. 1908. Type: *Pteris angustifolia* Sw. = *Ananthacorus angustifolius* (Sw.) Underw. & Maxon.

Epiphytic, the rhizome small, short-creeping, scaly, bearing the leaves in a loose cluster or spaced; leaves small, the lamina simple, entire, glabrous, veins anastomosing, forming a few series of areolae on each side of the costa; sporangia borne in a long sunken line along each of the intramarginal commissures, indusium absent. paraphyses present. — An American genus of 1 species.

Ananthacorus angustifolius (Sw.) Underw. & Maxon. Contrib. U. S. Nat. Herb. 10: 487. 1908. FIG. 170.

Pteris angustifolia Sw. Prod. 129. 1788. Type: "Jamaica and Hispaniola," (Fl. Ind. Occ. 3: 1599).

Vittaria costata Kze. Linnaea 9: 77. 1834. Type: Tocache, Huallaga, Peru, Jun. 1830, *Poeppig;* isotype: W! (At B, Kze. Anal. Pterid. t. 18, f. 2, is mounted in the herbarium and has the same data as the holotype written on it; it is probable that the figure was prepared from the holotype at LZ, now destroyed).

Rhizome scales brown to atropurpureous, linear to narrowly lanceolate-attenuate, clathrate, iridescent; leaf ca. 8-35 cm. long, the lamina coriaceous, narrow and tapering gradually to base and apex (sterile ones much smaller and relatively broader, often elliptical), nearly or quite sessile, straight to subfalcate, the costa extending to the apex; the fertile commissure continuous or irregularly discontinuous, sometimes the sporangia in short, interrupted lines.

Tropical America.
Epiphyte in forest, San Martin and Huánuco, ca. 650 m.

Specimens seen: SAN MARTIN: Tocache, *Poeppig* (W); Cerro Campana, Tarapoto, *Spruce 4670* (P). HUANUCO: Supte river, n. of Tingo María, *Stork & Horton 9598* (F, US); junction of Río Monzón and Río Huallaga, *Asplund 12678* (US).

30. POLYTAENIUM Desv. Mém. Soc. Linn. Paris 6: 218. 1827, not *Polytaenia* DC. 1829 *(heteronym).* Type: *Hemionitis lineata* Sw. = *Polytaenium lineatum* (Sw.) J. Sm. FIG. 171.

Epiphytic, the rhizome small, short-creeping, scaly, bearing the leaves in a loose cluster; leaves small, the lamina simple, entire, glabrous, veins anastomosing, forming a few to many series of areolae on each side of the costa; sporangia more or less sunken, borne in several long lines, or along most of the veins, indusium and paraphyses absent. — An American genus of 10 species.

Benedict, R. C. The genus Antrophyum-I. Bull. Torrey Cl. 34: 445-458. 1907.

Benedict, R. C. The genera of the fern tribe Vittarieae. Bull. Torrey Cl. 38: 153-190. 1911.

Tryon, R. Taxonomic fern notes, IV. — Some American vittarioid ferns. Rhodora 66: 110-117. 1964.

This genus is frequently treated as part of the larger, predominantly Old World, *Antrophyum.* The reasons for maintaining it, largely on the bases of geography and the absence of paraphyses in *Polytaenium*, are discussed at length in my paper cited above, as are the changes in the application of names that are necessary.

The three species with a broad lamina require additional study before their classification can be considered to be adequate. The petiole color is not always easy to determine in dried specimens and if this character does not actually correlate as well as it seems to with the others some change in the classification may be necessary. Although material from Central America, of this group, and that from the Guianas is relatively uniform, there is greater variation and less correlation of characters in the central Andes. The rhizome scales of *Polytaenium* are brown, clathrate and sometimes iridescent; they are sometimes pectinate-toothed. The scales may offer some useful characters; however, the differences I have observed in South America do not correlate with other characters.

FIG. 171. *Polytaenium guayanense*. Rio Monzon, Tingo Maria (Huánuco).

KEY TO SPECIES

a. Soral lines few and long, parallel to the costa and deeply sunken in the tissue; lamina narrowly elliptic-linear. .... 1. *P. lineatum*

a. Soral lines many, long and short, divergent from the costa and superficial to partially sunken in the tissue. .... b.

  b. Petiole greenish beneath (or drying to light or dark brown), concolorous, or darker than the adjacent leaf-tissue, usually strongly alate; lamina usually coriaceous, broadly to narrowly oblanceolate. .... 2. *P. cajenense*

  b. Petiole pale (straw-colored) beneath (or drying lighter than the adjacent leaf-tissue); lamina usually papyraceous. .... c.

    c. Lamina rather narrowly elliptical or with nearly parallel sides, petiole narrowly alate. .... 3. *P. guayanense*

    c. Lamina oblanceolate, petiole strongly alate. .... 4. *P. brasilianum*

1. **Polytaenium lineatum** (Sw.) J. Sm. Jour. Bot. Hooker, 4: 68. 1841. FIG. 172.

Hemionitis lineata Sw. Prod. 129. 1788. Type: Jamaica, *Swartz;* isotype: Herb. Willd. 20033, B! photo GH.

Vittaria lanceolata Sw. Ges. Naturf. Freunde Berl. Mag. 2: 133. 1799, based on *Hemionitis lineata* Sw., not *Vittaria lineata* (L.) J. E. Sm.

Antrophyum lineatum (Sw.) Kaulf. Enum. Fil. 199. 1824.

Polytaenium lanceolatum (Sw.) Desv. Mém. Soc. Linn. Paris 6: 218. 1827.

Leaves ca. 8-30 cm. long, petiole strongly alate, straw-colored to light green beneath, concolorous with the adjacent leaf-tissue; lamina narrowly elliptic-linear, more or less coriaceous; soral lines few, long and parallel to the costa.

Tropical America.

Epiphyte in woods and forests, Huánuco, Junín and Ayacucho, 400-1800 m.

Specimens seen: HUANUCO: Muña, *Bryan 529* (F, US). JUNIN: Oxapampa, *Soukup 2352* (GH); Huacapistana, *Killip & Smith 24310* (US); near La Merced, *Killip & Smith 23859* (US). AYACUCHO: Río Apurímac valley, near Kimpitiriki, *Killip & Smith 22869* (US).

2. **Polytaenium cajenense** (Desv.) Benedict, Bull. Torrey Cl. 38: 169. 1911. FIG. 173.

Hemionitis cajenensis Desv. Ges. Naturf. Freunde Berl. Mag. 5: 311. 1811. Type: French Guiana, Herb. Desv., P!

Antrophyum cajenense (Desv.) Spreng. Syst. Veg. 4: 67. 1827.

Antrophyum discoideum Kze. Bot. Zeit. 6: 702. 1848. Lectotype: Colombia, *Karsten 30;* isotype: B! photo GH.

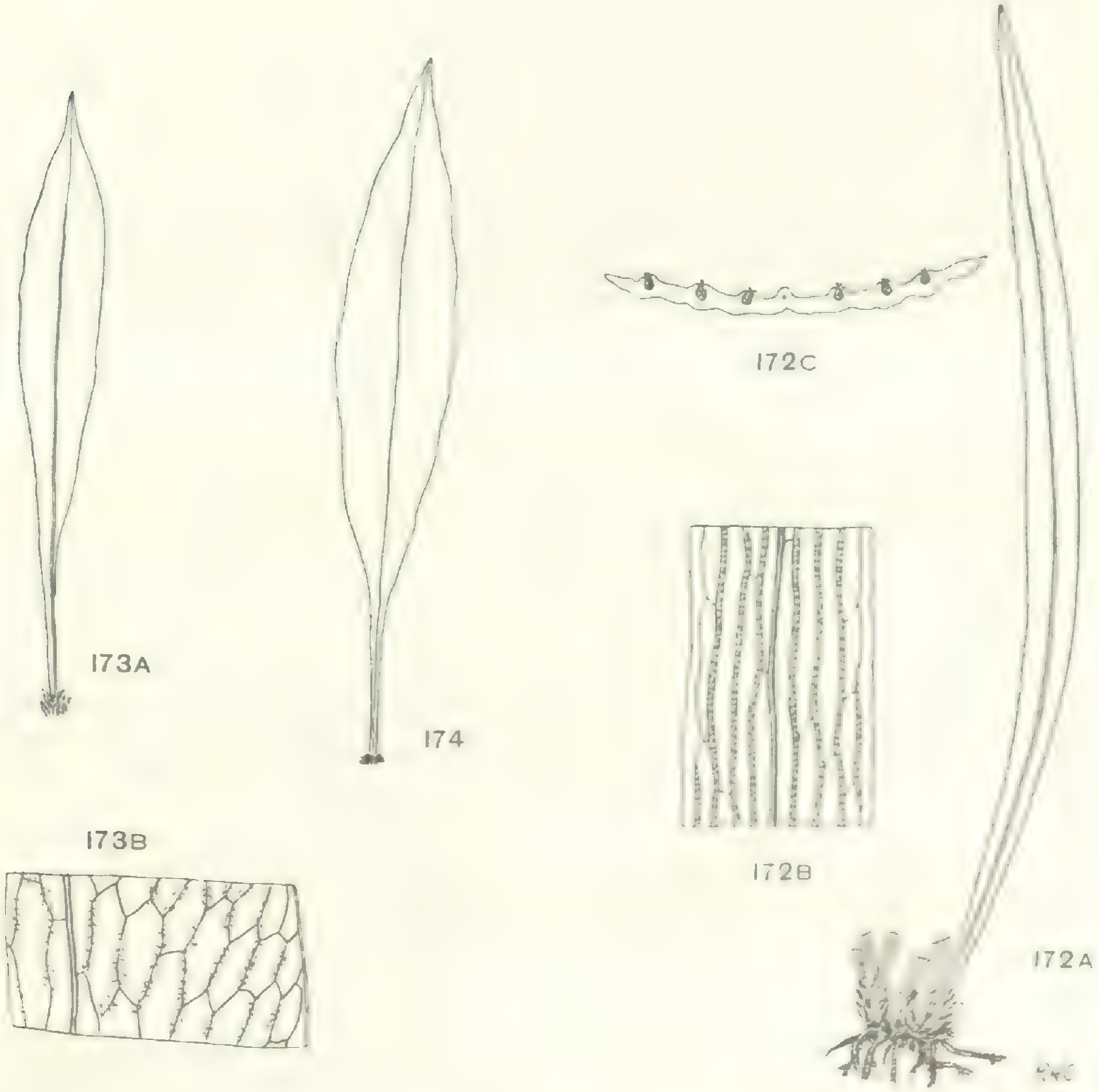
Polytaenium discoideum (Kze.) Benedict, Bull. Torrey Cl. 38: 169. 1911.

Leaves ca. 10-35 cm. long, petiole usually strongly alate, greenish beneath (drying to light or dark brown), concolorous with, or darker than, the adjacent leaf-tissue; lamina narrowly to broadly oblanceolate, papyraceous to usually coriaceous; soral lines many, following nearly all of the veins.

This species has usually been called *Polytaenium* (or *Antrophyum*) *brasilianum.*

Guatemala to Panama; Greater Antilles; Guianas to Colombia, south to Bolivia; Brazil.

Epiphyte in dense forest, Loreto, Huánuco and Cuzco, 100-1200 m.



FIGS. 172-174. Fig. 172. ***Polytaenium lineatum:*** A, plant, × ½, Brazil, ***Dusén 14886,*** GH; B, portion of fertile lamina, × 1¼, Colombia, *Lindig* 17[illegible], GH; C, section of fertile lamina, × 3, *idem.* Fig. 173. *P. cajenense:* A, leaf, × ¼, Peru, *Schunke* 28[illegible], GH; B, portion of fertile lamina, × 1, *idem.* Fig. 174. *P. guayanense:* leaf, × ¼, British Guiana, ***A. C. Smith 2872,*** GH.

Selected specimens: LORETO: Gamitanicocha, Río Mazán, *Schunke 283* (F, GH, US); San Antonio, Río Itaya, *Killip & Smith 29367* (US). HUANUCO: Hacienda Mercedes, prov. Huánuco, *Mexia 8177a* (GH); Tingo María, *Asplund 12222* (US), *Ferreyra 10230* (GH, USM), *Woytkowski 1097* (GH, USM). CUZCO: Hacienda Potrero, near Quillabamba, *Coronado 120* (GH, US).

3. **Polytaenium guayanense** (Hieron.) Alston, Kew Bull. 1932: 314. FIGS. 171, 174.

Antrophyum guayanense Hieron. Hedwigia 57: 212. 1915. Lectotype: Trinidad, *Fendler 151*, B!; isotype: GH!

Leaves ca. 10-30 cm. long, petiole narrowly alate, straw-colored beneath (or darker in drying but lighter than the adjacent leaf-tissue); lamina rather narrowly elliptical or with nearly parallel sides, subcoriaceous to usually papyraceous; soral lines many, following nearly all of the veins.

This species has usually been called *Polytaenium* (or *Antrophyum*) *cajenense.*

Guianas, Trinidad to Colombia and Peru, adjacent Brazil.

Epiphyte in forest, San Martín, Loreto and Huánuco, 135-800 m.

Specimens seen: SAN MARTIN: Tarapoto, *Spruce 3993* (P). LORETO: Santa Rosa, Río Huallaga below Yurimaguas, *Killip & Smith 28951* (GH, US). HUANUCO: Río Monzon, near Tingo María, *Tryon & Tryon 5300* (GH, U, US, USM).

4. **Polytaenium brasilianum** (Desv.) Benedict, Bull. Torrey Cl. 38: 169. 1911.

Hemionitis brasiliana Desv. Mém. Soc. Linn. Paris 6: 216. 1827. Type: Brazil, Herb. Desv. P! photo GH, US.

Antrophyum subsessile Kze. Anal. Pterid. 29. 1837. *(nom. superfl. illegit.)*. Type: the same as that of *Hemionitis brasiliana.*

Antrophyum brasilianum (Desv.) C. Chr. Ind. Fil. 59. 1905.

Leaves ca. 10-30 cm. long, petiole strongly alate, straw-colored beneath (or darker in drying but lighter than the adjacent leaf-tissue); lamina oblanceolate, papyraceous; soral lines many, following nearly all of the veins.

This species is not known from Peru but it has been collected in Bolivia and it may be expected to occur in the Department of Puno or Cuzco. It has previously usually been called *Polytaenium* (or *Antrophyum*) *discoideum.*

31. ANETIUM Splitg. Tijdsch. Nat. Gesch. 7: 395. 1840. Type: *Acrostichum citrifolium* L. = *Anetium citrifolium* (L.) Splitg.

Pteridanetium Copel. Gen. Fil. 224. 1947, based on *Anetium* Splitg. not *Anetia* Endl. *(heteronym).*

Epiphytic, the rhizome slender, long-creeping, scaly, bearing the leaves at intervals; leaves small to rarely large, the lamina simple, entire, glabrous, veins anastomosing, forming many series of areolae on each side of the costa; sporangia borne superficially and sparingly along the veins and also between them, indusium and paraphyses absent. — An American genus of 1 species.

C. V. Morton (Amer. Fern Jour. 43: 71. 1953) has pointed out that *Anetium* is a different name than *Anetia*, not a homonym of it as Copeland considered it to be.

Anetium citrifolium (L.) Splitg. Tijdsch. Nat. Gesch 7: 395. 1840. FIG. 175.

Acrostichum citrifolium L. Sp. Pl. 2: 1067. 1753. Type: Martinique, Plumier, Fil. t. 116.

Pteridanetium citrifolium (L.) Copel. Gen. Fil. 224. 1947.

Rhizome scales brownish, mostly broadly ovate-attenuate, clathrate, iridescent; leaves herbaceous-fleshy (papyraceous in drying), pendent, 10 to usually 15-30 to 100 cm. long, the lamina elliptical, to oblanceolate to ligulate, narrow to broad, nearly or quite sessile to short-petioled (especially in large leaves) the margin sometimes ruffled, costa extending ca. ¾ths the length of the lamina, apex obtuse to acute to abruptly acuminate.

Tropical America.

Epiphyte in dense forests, Loreto and Huánuco, 100-800 m.

Specimens seen: LORETO: Santa Rosa, below Yurimaguas, *Killip & Smith 28881* (US); Puerto Arturo, Río Huallaga, below Yurimaguas, *Killip & Smith 27900* (F, GH, US); Río Mazán, *Schunke 301* (F, GH, US). HUANUCO: Río Monzon, near Tingo María, *Tryon & Tryon 5300 1/2* (GH).

TRIBE 9. DAVALLIEAE.

32. NEPHROLEPIS Schott, Gen. Fil. no. 3. 1834. Type: *Polypodium exaltatum* L. = *Nephrolepis exaltata* (L.) Schott.

Terrestrial or epiphytic, the rhizomes small to rather stout, erect, usually stoloniferous, scaly, bearing the leaves in a crown or loose cluster; leaves of medium size to very long, 1-pinnate, glabrous, slightly scaly or pubescent, the pinnae articulate, veins free; sori orbicular to lunate, borne on the anterior branch of a vein, toward the margin, not paraphysate, indusium orbicular, attached at the base of the narrow sinus, to lunate and attached along the basal side. — 6 species in America.

Maxon, W. R. Pteridophyta (Nephrolepis), *in* Sci. Surv. Porto Rico & V. I. 6: 484-486. 1926.

Morton, C. V. Observations on Cultivated ferns, V — The species and forms of Nephrolepis. Amer. Fern Jour. 48: 18-27. 1958.

The species are terrestrial or casually epiphytic. In the latter case or when they grow on the edge of a bank, some, such as *N. biserrata* and *N. cordifolia,* may develop very long leaves (up to 3 or 4? m.). In many specimens of these species, regardless of the length of the leaf, the apex is a loose bud and the leaf is thus apparently indeterminate. In other specimens the apex is fully expanded but usually not well developed.

Many species of *Nephrolepis* are cultivated and several of them are represented by variants that depart rather widely from the wild form. The recent paper by C. V. Morton, cited above, treats the kinds that are commonly cultivated and includes references to other more detailed treatments. Here I have included only the two exotic cultivars that have evidently escaped from cultivation in Peru.

KEY TO SPECIES

a. Indusia orbicular to orbicular-reniform, at least toward the base of the pinna (rarely all reniform in no. 2), mostly facing the margins of the pinna, the sinus narrow to U-shaped; vascular bundles, above the base of the petiole, 3-7. .... b.
  b. Pinnae simple. .... c.
    c. Pinnae, the basal ones excepted, with the base very unequal, cuneate to convexly so on the inferior side, acutely to subacutely auriculate on the superior side; pinnae minutely appressed-squamulose beneath; vascular bundles 3-5. .... 1. *N. rivularis*
    c. Pinnae with the base rather equally cuneate to equally auriculate, or somewhat unequal and rounded on the inferior side; pinnae commonly hirtellous or fibrillose-squamulose beneath (or both). .... d.
      d. Longer pinnae rather abruptly reduced to a prolonged apex, to acuminate; indusia all orbicular, with a very narrow sinus; pinnae commonly hirtellous beneath, very rarely only squamulose; vascular bundles 5-7. .... 3. *N.biserrata*
      d. Longer pinnae obtuse to shortly acute; indusia variable, at least some toward the base of the pinna orbicular to orbicular-reniform, at least some toward the apex reniform to lunate (rarely all reniform); commonly squamulose or glabrate beneath; vascular bundles 3 (-5). .... 2. *N. exaltata*
  b. Pinnae, or at least some of them, pinnatifid or more complex. .... 2a. *N. exaltata* cv. *Bostoniensis*

a. Indusia reniform to lunate, mostly facing the apex of the pinna, the sinus broad or absent, the mature sporangia projecting on the open side; vascular bundles, above the base of the petiole, 1-3. .... e.

e. Pinnae simple and orbicular, or with two lobes. .... 4a. *N. cordifolia* cv. *Duffii*

e. Pinnae simple and elongate. .... f.

f. Upper pinnae, but not necessarily the apical ones, rounded at the base on the inferior side (sometimes shortly so) to all pinnae cordate; vascular bundles 1-3. .... g.

g. Pinnae coriaceous, the veins obscure, rarely thin and the veins evident; stolons wiry and relatively stout, usually numerous, often tuber-bearing (but not native plants in Peru); plant developing a substantial rhizome. .... 4. *N. cordifolia*

g. Pinnae thin-herbaceous, the veins evident; stolons rather soft, slender, usually few, usually or always tuber-bearing; plant apparently annual from a tuber, only a small rhizome developed. .... 5. *N. occidentalis*

f. Upper pinnae cuneate at the base on the inferior side, or all pinnae except the basal ones so, auriculate on the superior side; vascular bundle 1; stolons not tuber-bearing. ...... 6. *N. pectinata*

1. **Nephrolepis rivularis** (Vahl) C. Chr. Ind. Fil. 455. 1906. FIG. 176.

Polypodium rivulare Vahl, Eclog. Amer. 3: 51. 1807. Type: Montserrat, West Indies, *Ryan.*

Aspidium eminens Wickstr. Vet. Akad. Handl. 1825: 436. 1826. Type: Guadeloupe, *Forsström*, S-PA!

Nephrodium crenatum Desv. Mém. Soc. Linn. Paris 6: 252. 1827. Type: "Trop. Amer." P, photo GH!

Nephrolepis intermedia Sod. Rec. Crypt. Vasc. Quit. 57. 1883. Type: San Miguel de los Colorados, Ecuador, *Sodiro;* isotype: K!; authentic specimens: UC! US!

Vascular bundles in the petiole, above the base, 3-5; pinnae sessile, very unequal at the base, the inferior side cuneate, the superior acutely auriculate, apex obtuse to acuminate, minutely appressed-squamulose beneath; indusium orbicular, mostly facing the margin of the pinna, sinus very narrow, the sporangia projecting on all sides when mature.

The combination *Nephrolepis rivularis* was not made by Krug (Engl. Bot. Jahrb. 24: 122. 1897) as commonly cited. It was definitely made, although unintentionally, by C. Christensen; it may also have been properly made earlier.

Tropical America.

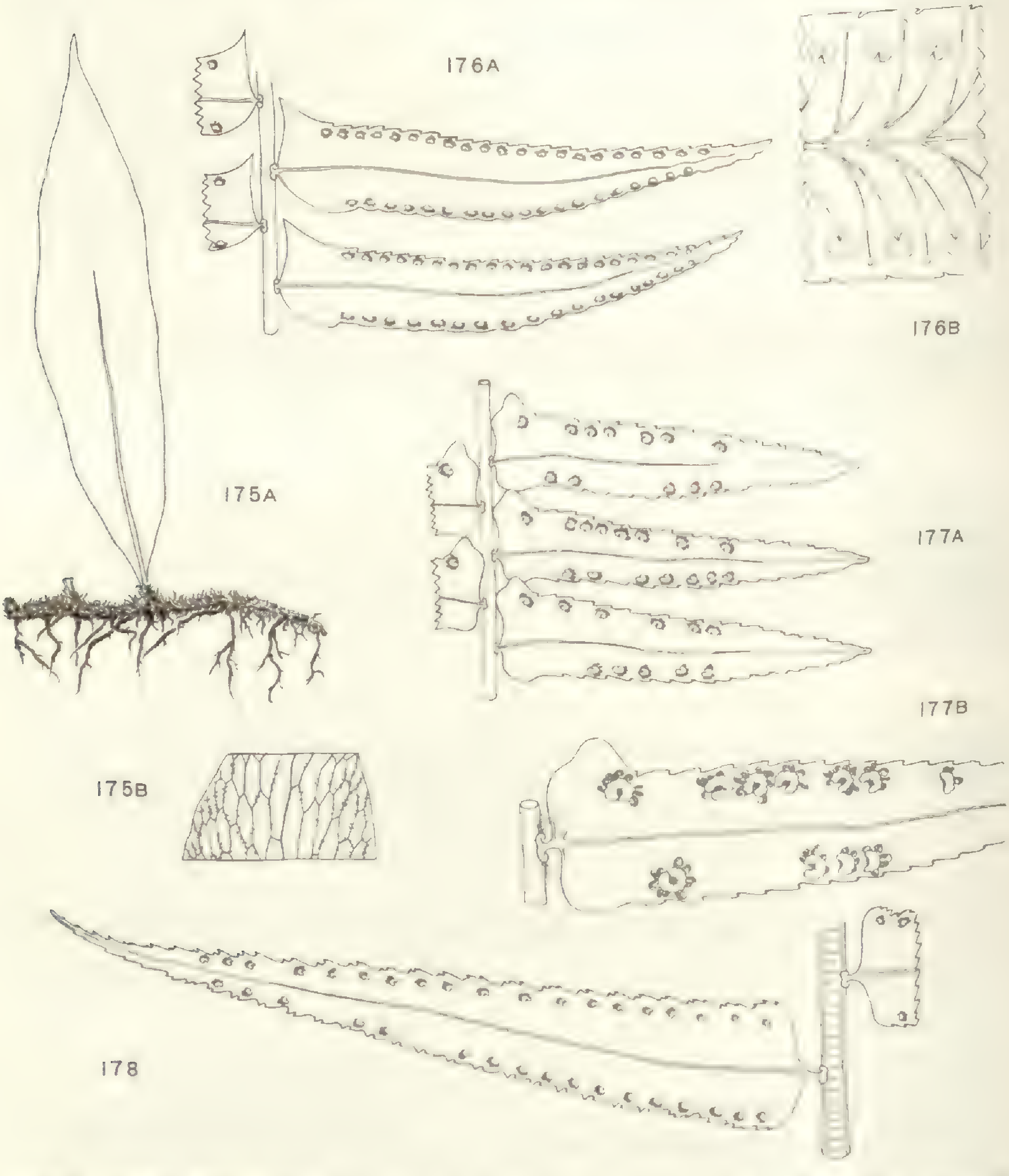
In forests, terrestrial and on tree bases, San Martín to Puno, 100-1000 m.

Specimens seen: SAN MARTIN: Soritor, *Woytkowski 6246* (GH). LORETO: Pinto-Cocha, Río Nanay, *L. Williams 812* (F, US); between Río Nanay and Río Napo, *L. Williams 703* (F); San Juan, Iquitos, *L.*

Williams 3733 (F); Mishuyacu, near Iquitos, *Klug 176* (F, US); Gamitanicocha, Río Mazán, *Schunke 219* (GH, UC). HUANUCO: Tingo María, *Allard 21492* (US). MADRE DE DIOS: Maldonado, *Rauh P751* (B). PUNO: San Gaban (Río), *Lechler 2515* (GH, K).

2. **Nephrolepis exaltata** (L.) Schott, Gen. Fil. no. 3. 1834. Fig. 177.
Polypodium exaltatum L. Syst. Nat. ed. 10, 2: 1326. 1759. Lectotype: (by Alston, Phil. Jour. Sci. 50: 182. 1933) Sloane, Jam. t. 31; Sloane Herb. 1: 52, BM!

Vascular bundles in the petiole, above the base, 3 to rarely 5; pinnae subsessile to petiolulate, usually rather unequal at the base, the inferior



Figs. 175-178. Fig. 175. *Anetium citrifolium:* A, plant, × ½. Jamaica, *Maxon & Killip 790*, GH; B, portion of fertile lamina, × 1, *idem*. Fig. 176. *Nephrolepis rivularis:* A, fertile pinnae, × 1½, Dominica, *Hodge & Hodge 1719*, GH; B, portion of fertile pinna, × 5, St. Lucia, *Howard 11385*, GH. Fig. 177. *N. exaltata:* A, fertile pinnae, × 1½, Porto Rico, *Holm 157*, GH; B, portion of fertile pinna, × 2½, *idem*. Fig. 178. *N. biserrata:* fertile pinna, × 1½, Guatemala, *Deam 478*, GH.

side rounded to auriculate, the superior side auriculate, the apex obtuse to acute, fibrillose-squamulose to glabrate beneath; indusium orbicular to orbicular-reniform toward the base of the pinna, to reniform or lunate toward the apex, the orbicular ones mostly facing the margin, the reniform and lunate ones facing the apex, mature sporangia mostly projecting on all sides.

The wild species is native to Florida, Central America, the West Indies and northern South America.

2a. **Nephrolepis exaltata cv. Bostoniensis.**

Nephrolepis exaltata var. *bostoniensis* Davenp. New England Florist 2: 137. 1896. Type: *from F. W. Fletcher*, Davenp. Herb., GH!

The Boston Fern and the many cultivars derived from it are commonly and widely cultivated. Discarded plants may persist and spread by means of the stolons in tropical and subtropical areas. The collections cited below are perhaps from such a source. I have not tried to identify the particular kind of Boston Fern that these specimens represent.

LORETO: Caballo-Cocha, *L. Williams 2381* (F): Yurimaguas, *L. Williams 4051, 4053, 4330* (F); Bersalles, prov. Iquitos, *Vargas 11471* (GH).

3. **Nephrolepis biserrata** (Sw.) Schott, Gen. Fil. no. 3. 1834. FIG. 178.

Aspidium biserratum Sw. Jour. Bot. Schrad. 1800(2): 32. 1801. Type: Mauritius, *Gröndat*, Herb. Sw. S-PA!

Tectaria fraxinea Cav. Descr. 250. 1802. Type: Obragillo, Peru, *Née*, MA, seen by C. Chr. (Dansk Bot. Ark. 9(3):15. 1937), and referred here.

Vascular bundles in the petiole, above the base, 5-7; pinnae petiolulate, more or less equally cuneate to equally auriculate at the base, the apex of the longer pinnae reduced to a prolonged apex to acuminate, fibrillose-squamulose beneath and also hirtellous, very rarely only scaly; indusium orbicular, mostly facing the margin of the pinna, the sinus narrow, the mature sporangia projecting on all sides.

The lamina of this species is usually considerably broader than that of any other one; even in rather small leaves it is rarely less than 15-20 cm. broad, and in larger leaves, some of which may be up to about 3 m. long, it is commonly 30-40 cm. broad.

The taxonomy of this species is not well understood. Although it is evidently distinct among other American species, it intergrades with the Asiatic *N. hirsutula* (Forst.) Presl, at least in the characters presently employed to distinguish the two. Also, the American material is very commonly hirtellous, while the Asiatic *N. biserrata* is very rarely hirtellous. The proper status and name of the American *N. biserrata* can be clarified only by a monographic study.

Tropical America; Old World.

In clearings, forests, or along forest borders, terrestrial or epiphytic, especially on palm trunks, San Martín, Loreto and Ayacucho, 100-900 m.

Selected specimens: SAN MARTIN: Rioja, *Woytkowski 6155* (GH); Tarapoto, *Spruce 4747* (K), *L. Williams 5449, 5615, 6581* (F), *Woytkowski 35230* (UC). LORETO: Iquitos, *Mexia 6489* (F, GH, UC, US), *Tryon & Tryon 5163, 5176* (BM, F, GH, U, US, USM). AYACUCHO: Kimpitiriki, Río Apurímac, *Killip & Smith 22856* (F, US).

4. **Nephrolepis cordifolia** (L.) Presl, Tent. Pterid. 79. 1836. **Fig. 179, Map 44.**

Polypodium cordifolium L. Sp. Pl. 2: 1089. 1753. Type: Petiver, Pterigraph. Amer. t. 1, fig. 11 (not seen in Petiver, Hort. Sicc. in Hb. Sloane, BM).

Aspidium tuberosum Willd. Sp. Pl. 5: 234. 1810. Type: Bourbon, Herb. Willd. 19759, B! photo GH.

Aspidium pendulum Raddi, Opusc. Sci. Bolog. 3: 289. 1819. Type: Brazil, *Raddi*, FI; isotype: "*Aspidium pendulum* Raddi" *ex Raddi*, K!

Nephrolepis pendula (Raddi) J. Sm. Jour. Bot. Hooker, 4: 197. 1841.

Vascular bundles in the petiole, above the base, 1-3; pinnae subsessile to petiolulate, rather unequal at the base, rounded, sometimes shortly so to semicordate on the inferior side, acutely to usually obtusely auriculate on the superior side, apex usually obtuse to acute, glabrous to rarely minutely fibrillose-squamulose beneath; indusium reniform to lunate, mostly facing the apex of the pinna, the mature sporangia projecting on the open side.

The Petiver illustration is not adequate for the purposes of accurate identification but I am applying the name in its usual sense.

Some epiphytic plants have very long, pendent leaves, up to 3 m. and perhaps longer. However, in comparison with the long leaves of *N. biserrata*, the lamina of those of *N. cordifolia* are narrow, about 8-10 cm. broad. I have seen no evidence of tubers on the stolons of Peru material; they are frequent on plants from the West Indies.

I have not been able to maintain the usually recognized

Maps 43-46. Map 43, *Vittaria*. Map 44, *Nephrolepis cordifolia*. Map 45, *N. pectinata*. Map 46, *Lindsaea*.

N. pendula, being unable to find any character by which it might be clearly distinguished. The tuber-bearing habit of *N. cordifolia* (in the West Indies, for example) is evidently not constant and the long pendent leaves of *N. pendula* (in South America) gradually grade into shorter and erect ones.

Tropical America; Old World.

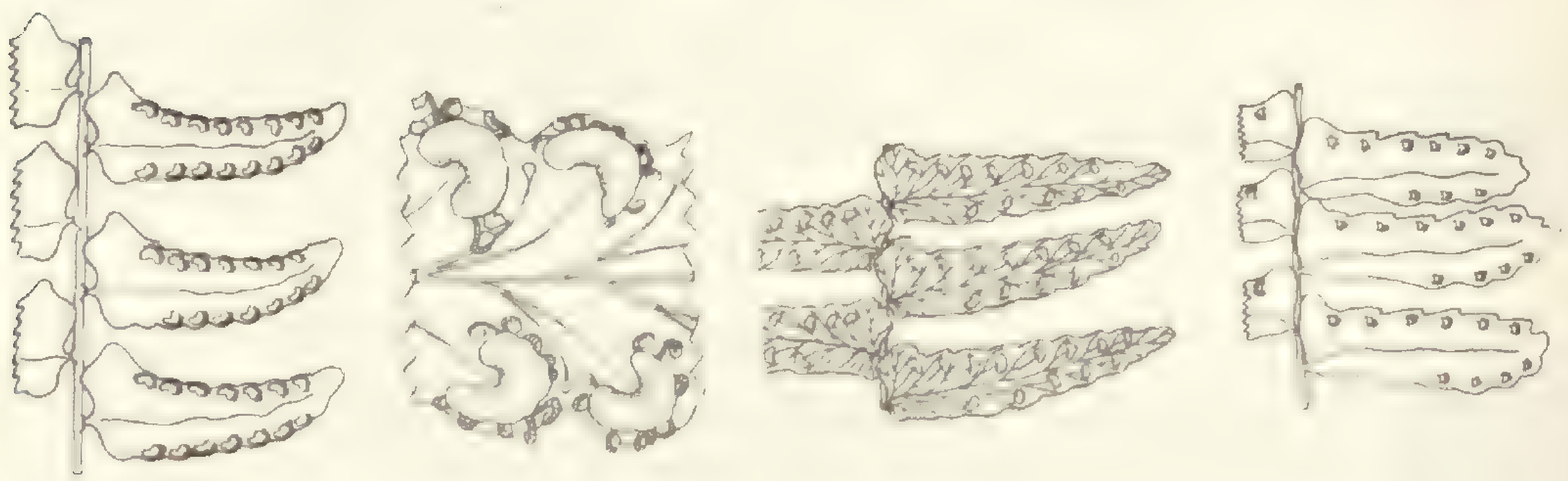
In dense forest, on shrubby slopes, rocky places and on road banks, Amazonas to Cuzco, 200-3500 m.

Selected specimens: AMAZONAS: Chachapoyas, *Mathews 3280* (K); entre Chachapoyas y Cáclic, *López et al. 4350* (GH). SAN MARTIN: Tarapoto, *L. Williams 6129* (F); Zepelacio, near Moyobamba, *Klug 3736* (F, GH, US). LORETO: Río Santiago, above Pongo de Manseriche, *Mexia 6163* (F, GH, UC, US); Boquerón del Padre Abad, *Ridoutt* (GH, USM). HUANUCO: Muña, *Macbride 4053* (F, US); Carpish Pass, *Coronado 71* (GH, UC); Tingo María, *Allard 20425, 22362* (US); Hacienda Paty, *Ferreyra 9353* (GH, USM). JUNIN: Huacapistana, *Ferreyra 11308* (GH, USM), *Cerrate 2886* (GH, USM), *Coronado 258* (GH, UC), *Tryon & Tryon 5452* (BM, F, GH, U, US, USM); near Perené Bridge, Río Paucartambo, *Killip & Smith 25383* (F, GH, US). AYACUCHO: Estrella, *Killip & Smith 22674* (F, US). CUZCO: Tambomayo, prov. Paucartambo, *West 7125* (UC); Machu-Picchu, *Vargas 3167* (F); Valle de Santa Ana, *Herrera 2627* (US).

4a. Nephrolepis cordifolia cv. Duffii.

Nephrolepis Duffii Moore, Gard. Chron. n.s. 9: 622, f. 113. 1878. Type: *Hort. Veitch, ex Duff*, Duke of York's Island, Territory of New Guinea, Herb. Moore, K!

In this unusual form, the pinnae are either orbicular or consist of two orbicular lobes, and the rachis is often dichotomously branched, sometimes several times. Widely culti-



FIGS. 179-181. Fig. 179. *Nephrolepis cordifolia:* A, fertile pinna, × 1½, Peru, *Tryon & Tryon 5452*, GH; B, portion of fertile pinna, × 5, *idem*. Fig. 180. *N. occidentalis:* fertile pinnae, × 1, Mexico, *Hinton 9341*, GH. Fig. 181. *N. pectinata:* fertile pinnae, × 1½, Colombia, *Haught 1934*, GH.

vated and evidently sometimes becoming established from discarded plants.

LORETO: Iquitos, *L. Williams 3578* (F); Pébas, Río Amazonas, *L. Williams 1825* (F).

5. **Nephrolepis occidentalis** Kze. Linnaea 18: 343. 1844. Type: *Leibold 27*, Mexico, LZ destroyed; *Leibold 127*, B! is this species. FIG. 180.

Vascular bundles in the petiole, above the base, 1-3; pinnae sessile or subsessile, unequal at the base, rounded to subauriculate on the inferior side, auriculate on the superior side, apex acute, glabrous to minutely glandular-pubescent beneath; indusium reniform to lunate, mostly facing the apex of the pinna, mature sporangia projecting on the open side.

The pinnae are usually long-triangular and thin in texture with the veins evident. The rhizome is poorly developed and evidently most plants are annual from a tuber. Some of the stolons of a mature plant always (?) bear tubers.

Mexico to Panama: Greater Antilles; Colombia, Venezuela, Peru and Brazil.

Rocky mountain side, Huánuco, 2100 m.

Specimens seen: HUANUCO: Muña, *Bryan 415* (F, GH).

6. **Nephrolepis pectinata** (Willd.) Schott, Gen. Fil. no. 3. 1834. FIG. 181, MAP 45.

Aspidium pectinatum Willd. Sp. Pl. 5: 223. 1810. Type: Herb. Willd. 19753, B! photo GH.

Vascular bundle in the petiole, above the base, 1; pinnae sessile or subsessile, very unequal at the base, cuneate on the inferior side, auriculate on the superior side, apex obtuse to shortly acute, glabrous beneath; indusium reniform to lunate, mostly facing the apex of the pinna, mature sporangia projecting on the open side.

The type of Willdenow's name has been uncertain due to the fact that his citation of "*Aspidium trapezoides* Schkuhr" has been taken to refer to a latter homonym of *Aspidium trapezoides* Sw. If this were true, the type of *Aspidium pectinatum* would be the type of *Aspidium trapezoides* Schkuhr. However, a study of Schkuhr's treatment clearly shows that he was using Swartz's name and hence Willdenow's reference to it, rather than to Swartz, must be taken as a reference to the taxon and not to the name. *Aspidium* *pectinatum* Willd. is a new species and typified by Willdenow's material.

Mexico to Panama; Greater Antilles; Colombia to Bolivia.

In forests, ravines, on stream banks, often on rocks or a low epiphyte on trees, San Martín to Puno, 200-2900 m.

Selected specimens: SAN MARTIN: Tarapoto, *Spruce 4082* (BM); Ekin, Tarapoto, *Woytkowski 35245* (UC); San Roque, *L. Williams 7517* (F, US). LORETO: above Pongo de Manseriche, *Mexia 6219* (F, GH, UC, US); Pumayacu, between Balsapuerto and Moyobamba, *Klug 3246* (F, GH, US). HUANUCO: above Cayumba, Río Huallaga, *Mexia 8324* (F, GH, UC, US); Hacienda Exito, *Mexia 8135* (F, GH, UC, US); Tingo María, *Ferreyra 10228* (GH, USM). JUNIN: Satipo, *Ridoutt* (GH, USM); Pichis Trail, *Killip & Smith 25506, 25859* (F, US); above San Ramón, *Killip & Smith 24613* (F, GH, US). CUZCO: Cosñipata, *Vargas 10217* (UC); San Pedro, prov. Quispicanchi, *Vargas 9748* (GH). PUNO: La Pampa, prov. Sandia, *Watkins* (US); San Gaban (Río), *Lechler 2155* (B, K), *3313* (B).

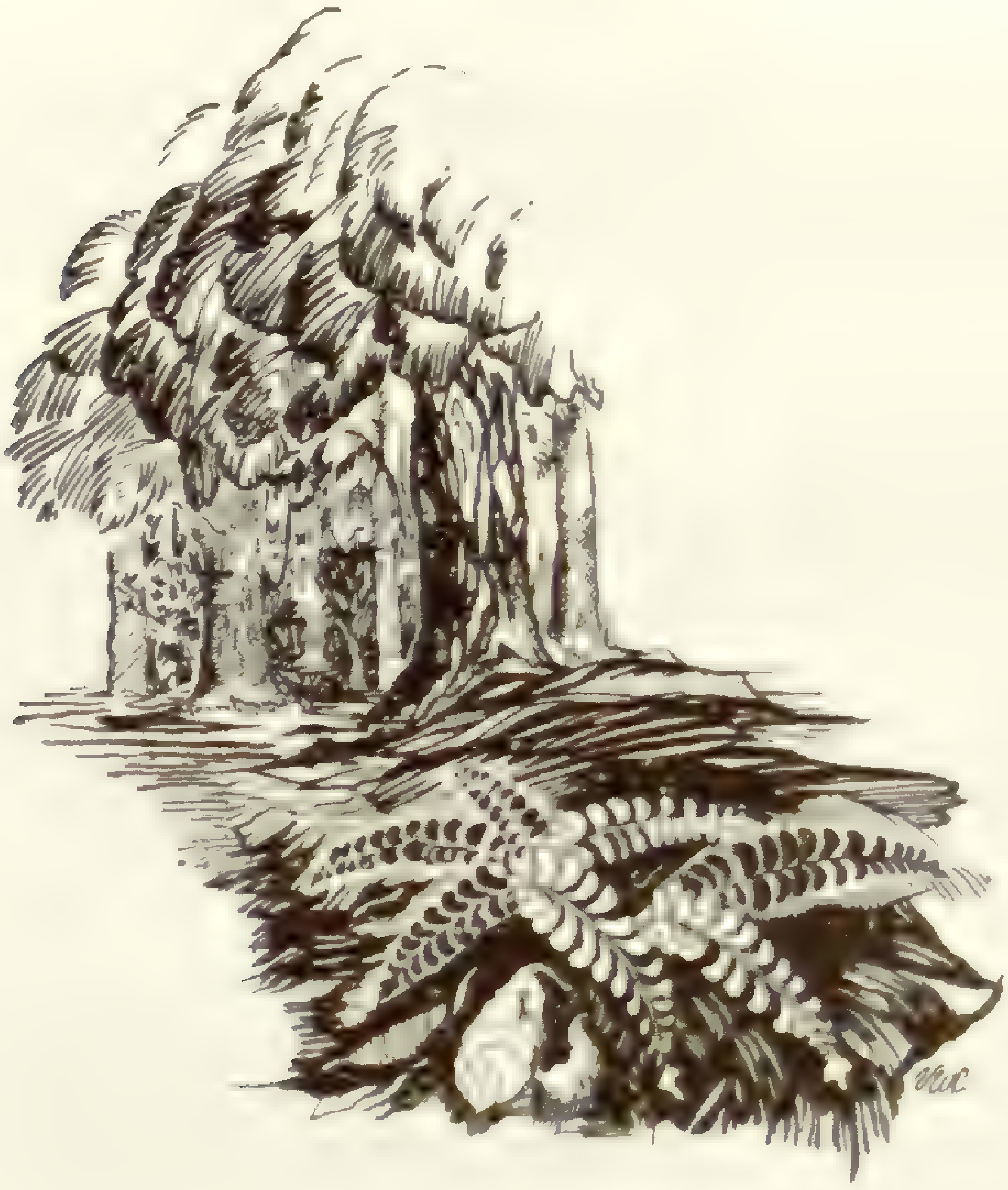


FIG. 182. *Lindsaea lancea* var. *falcata*, Tingo María (Huánuco).

TRIBE 10. LINDSAEEAE.

33. **Lindsaea** J. E. Sm. Mém. Acad. Turin 5: 401. 1793. Type: *Lindsaea trapeziformis* Dryand. = *Lindsaea lancea* (L.) Bedd. **Fig. 182, Map 46.**

Terrestrial, the rhizome slender to rather stout, short-creeping or decumbent, scaly, bearing the leaves in a usually loose cluster; leaves small to large, 1-pinnate to bipinnate, glabrous, veins free; sorus borne on a long marginal commissure connecting the vein-tips, not paraphysate (minute trichomes may be present), indusium attached along the commissure, opening toward the nearly plane and unmodified margin. — 46 American species.

Kramer, K. U. A revision of the genus Lindsaea in the New World. Acta Bot. Neerland. 6:97-290. 1957.

The treatment of this genus has been adapted with the aid of K. U. Kramer from his monograph cited above. Most of the materials have been cited from his revision; to these I have added a few of my own identifications of recently acquired material. The center of species of *Lindsaea*, both in number and abundance, is in northern South America. A little over 1/5th of the American species grow in Peru but they have not been commonly collected. They are often quite local in areas where suitable habitats seem to be frequent.

KEY TO SPECIES

a. Apical pinnules (apical pinnae of 1-pinnate laminae) strongly reduced, the terminal segment small and more or less confluent with the adjacent lateral ones. .... b.
  b. Lamina bipinnate and the pinna-rachises with lateral wings or angles on the abaxial side that are lighter in color than the pinna-rachis proper. .... c.
    c. Pinna-rachises with the wings continuous at their base, pinnae spreading. .... 3. *L. divaricata*
    c. Pinna-rachises with the wings or angles irregularly interrupted at their base, pinnae strongly ascending. .... 5. *L. portoricensis*
  b. Lamina 1-pinnate, or bipinnate and the pinna-rachises lacking wings or angles on the abaxial side, or they are present and concolorous with the pinna-rachis proper. .... d.
    d. Ultimate segments (pinnae or pinnules) mostly 3 or more times as long as broad. .... e.
      e. Largest ultimate segments 15 mm. or more long. .... 1. *L. arcuata*
      e. Largest ultimate segments 5-9 mm. long. .... 2. *L. Spruceana*
    d. Ultimate segments (pinnules or pinnae) mostly 2¼ times or less as long as broad. .... f.

f. Indusium 0.15 mm. wide, entire to minutely erose, segments herbaceous, veins evident. .... 4. *L. guianensis* ssp. *guianensis*

f. Indusium ca. 0.3-0.5 mm. wide, repand-erose to strongly erose or lacerate. .... g.

g. Segments firmly herbaceous to chartaceous, veins usually evident; indusium ca. 0.3 mm. wide, mostly repand-erose. .... 5. *L. portoricensis*

g. Segments usually coriaceous, veins obscure; indusium 0.3-0.5 mm. wide, mostly strongly erose to lacerate. .... 6. *L. stricta*

a. Apical pinnules (apical pinnae of 1-pinnate laminae) but little reduced, the terminal segment large, free or nearly so from the adjacent lateral ones. .... h.

h. Petiole rounded on the abaxial side; castaneous to blackish, pinna-rachises with pale lateral wings. .... 3. *L. divaricata*

h. Petiole angular or winged on the abaxial side, at least toward the apex. .... i.

i. Terminal segment of the lamina (or of the pinnae in bipinnate laminae) acute or subacute. .... 7. *L. lancea*

i. Terminal segment of the lamina (or of the pinnae in bipinnate laminae) very obtuse to concave. .... j.

j. Terminal segment flabellate, petiole reddish to dark brown. .... 8. *L. Schomburgkii*

j. Terminal segment triangular-cuneate or crescent-shaped, petiole stramineous to pale brown. .... k.

k. Ultimate segments 3 to 4 times as long as broad, usually dark olivaceous to brown when dry. .... 9. *L. latifrons*

k. Ultimate segments 4 to 6 times as long as broad, usually bright green when dry. .... 10. *L. hemiglossa*

1. **Lindsaea arcuata** Kze. Linnaea 9: 86. 1834. Type: Pampayacu, Peru, *Poeppig 1133,* LZ, destroyed; probable isotype: B. FIG. 183.

Petiole ca. 10-40 cm. long, stramineous to pale brown, the abaxial side rounded to usually angular or sulcate; lamina 1-pinnate or bipinnate, ca. 10-45 cm. long, apical pinnae (or apical pinnules of bipinnate laminae) reduced to the small, lanceolate terminal segment which is more or less confluent with the lateral segments adjacent to it, rachis of 1-pinnate laminae abaxially angular, sulcate, pinna-rachises abaxially rounded at the base, becoming concolorously angled beyond, ultimate segments 3 to 3½ times as long as broad, 12-35 mm. long, herbaceous, the veins evident to rather obscure; indusium ca. 0.2 mm. wide, subentire.

Mexico to Costa Rica; Greater Antilles; Venezuela to Bolivia; Brazil.

Dense forest, Loreto to Cuzco, 100-1500 m.

Specimens seen: LORETO: Tierra Doble, alto Río Nanay, *L. Williams 1071* (F, US). HUANUCO: Pampayacu, *Kanehira 177* (GH, US), *Poeppig*

(B). JUNIN: Yapas, Pichis Trail, *Killip & Smith 25522* (F, NY, US); Villa Amoretti, *G. Kunkel 578* (GH). CUZCO: Bajada, Río Tocate, *Bües 1739* (US).

2. **Lindsaea Spruceana** Kuhn, Linnaea 36: 79. 1869. Type: Mt. Guayrapurima, Tarapoto, Peru, *Spruce 4023*, B; isotypes: BM, BR, F, G, GH, K, LE, W. FIG. 184.

Lindsaea tarapotensis C. Chr. Ind. Fil. 398. 1906, based on *Lindsaea Spruceana* Kuhn.

Petiole 2-9 cm. long, stramineous to pale reddish-brown, the abaxial side angled to rounded; lamina 1-pinnate or bipinnate, 8-16 cm. long, apical pinnae (or apical pinnules of bipinnate laminae) reduced to the small, lanceolate-linear terminal segment which is more or less confluent with the lateral segments adjacent to it, rachis of 1-pinnate laminae and pinna-rachises abaxially concolorously angular or sulcate, largest ultimate segments 3 to 3½ times as long as broad, 5-9 mm. long, herbaceous, the veins obscure; indusium 0.15-0.25 mm. wide, sub-entire.

This species may be only a dwarf form of the former one, *L. arcuata.* Additional material is needed in order to assess its status properly.

Peru.

San Martín.

Specimens seen: SAN MARTIN: Mt. Guayrapurima, near Tarapoto, *Spruce 4023* (B, BM, F, G, GH, K, LE, W).

3. **Lindsaea divaricata** Kl. Linnaea 18: 547. 1845. Type: British Guiana, *Schomburgk 368*, B. FIG. 185.

Petiole ca. 10-60 cm. long, castaneous to nearly black, the abaxial side rounded; lamina bipinnate, ca. 20-90 cm. long, apical pinnules reduced, or not, to the small to moderately large, triangular-lanceolate terminal segment which is more or less confluent with, or free from, the lateral segments adjacent to it, pinna-rachises abaxially with continuous pale wings beyond the base, ultimate segments ca. 2½ times as long as broad, ca. 10-20 mm. long, herbaceous, the veins usually obscure; indusium 0.10-0.15 mm. wide, entire or subentire.

The pinnae which are laxly spreading at an angle of about 45-60 degrees afford a useful character for the distinction of some specimens of this species from some of those of *L. portoricensis.* In that species the pinnae are strongly ascending.

Mexico to Panama; Lesser Antilles; Guianas and Brazil to Colombia, Venezuela, Bolivia and Paraguay.

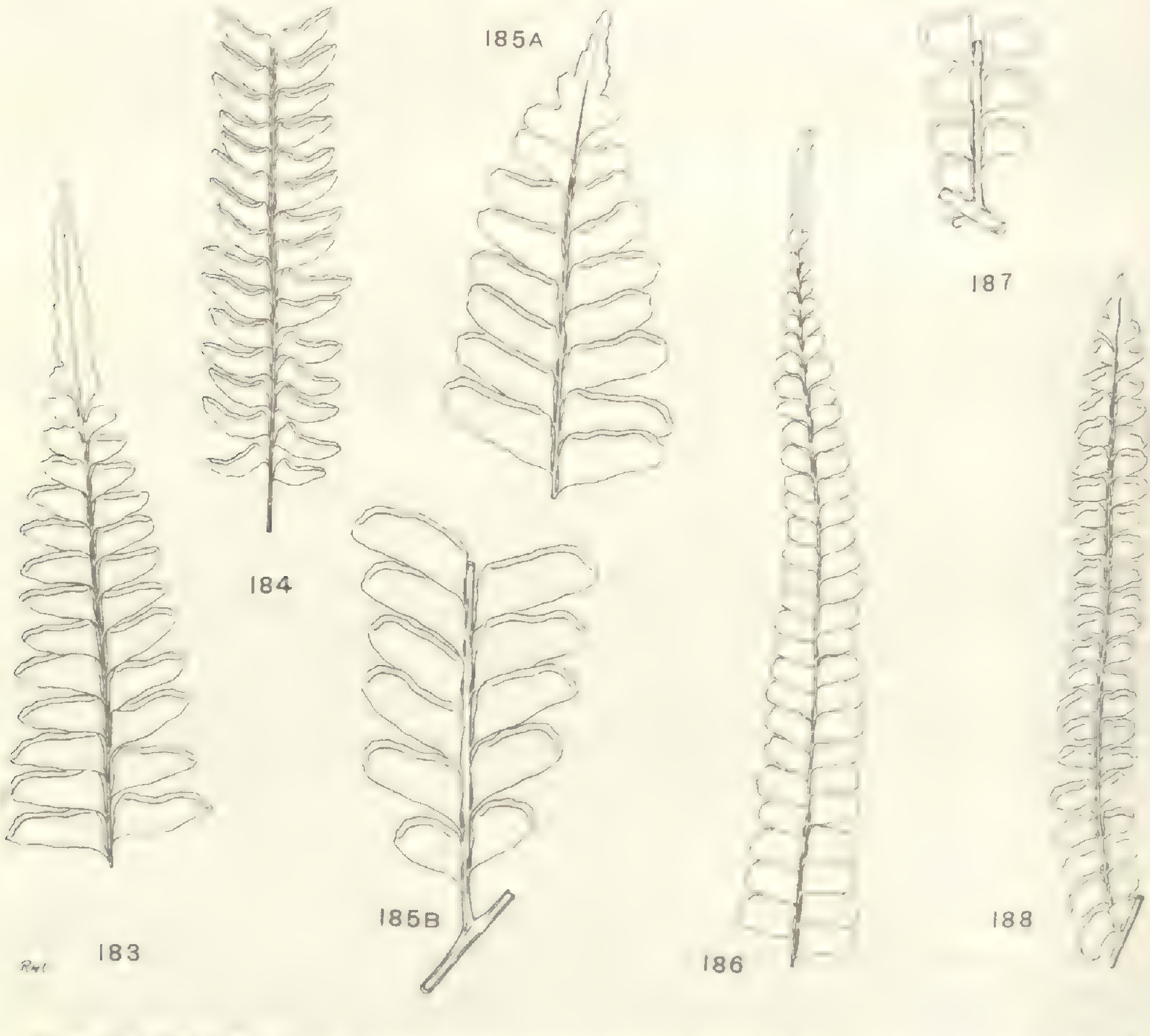
Dense forest and hillside forest, Loreto and Huánuco, 100-750 m.

Specimens seen: LORETO: mouth of Río Santiago, *Mexia 6133b* (UC, US); near Iquitos, *Klug 69, 1337* (F, NY, US). HUANUCO: Tingo María, *Tryon & Tryon 5339* (F, U, USM), *Aguilar 301*, in part (UC).

4. **Lindsaea guianensis** (Aublet) Dryand. Trans. Linn. Soc. 3: 42. 1797, ssp. **guianensis.** FIG. 186.

Adiantum guianense Aublet, Hist. Pl. Guian. 2: 963. 1775. Type: French Guiana, *Aublet*, P?

Petiole ca. 10-60 cm. long, stramineous to rarely castaneous beyond the dark brown to blackish base, the abaxial side rounded; lamina usually bipinnate, rarely 1- pinnate, ca. 20-65 cm. long, apical pinnules (or apical pinnae of 1-pinnate laminae) reduced to the small, lanceolate-linear, often caudate, terminal segment which is more or less confluent with the lateral segments adjacent to it, rachis of 1-pinnate laminae concolorously angled or winged, pinna-rachises abaxially rounded (always so at the base) to concolorously angled or sulcate, largest ultimate segments ca. 2 times as long as broad, ca. 10-12 mm.



FIGS. 183-188. Fig. 183. *Lindsaea arcuata:* apical half of fertile pinna, × 1. Brazil, *L. B. Smith 1965*, GH. Fig. 184. *L. Spruceana:* basal portion of lamina, × 1½, Peru, *Spruce 4023*, GH. Fig. 185. *L. divaricata:* A, apex of fertile pinna, × 1, Bolivia, *Steinbach 5309*, GH; B, base of fertile pinna, × 1, *idem*. Fig. 186. *L. guianensis* ssp. *guianensis:* apical half of pinna, × 1, Colombia, *Killip & Smith 14873*, GH. Fig. 187. *L. portoricensis:* base of fertile pinna, × 1, British Guiana, *Gleason 603*, GH. Fig. 188. *L. stricta* var. *stricta:* fertile pinna, × 1, Brazil, *Mexia 5486*, GH.

long, herbaceous, the veins evident; indusium ca. 0.15 mm. wide, entire to usually minutely erose-denticulate.

This subspecies has long-acuminate pinnae with the apical pinnules minute (1-2 mm. long); subspecies *lanceastrum* Kramer, of Brazil and Paraguay, has acute to short-acuminate pinnae with the apical pinnules longer (ca. 5 mm. long).

Nicaragua; Lesser Antilles; Guianas and northern Brazil to Venezuela, Colombia and Peru.

Hillside forest, Huánuco, 750 m.

Specimens seen: HUANUCO: Tingo María, *Tryon & Tryon 5275* (F, U, USM), *5289* (BM, F, GH, MO, U, US, USM), *Allard 21502* (US).

5. **Lindsaea portoricensis** Desv. Ges. Naturf. Freunde Berl. Mag. 5: 326. 1811. Type: Herb. Desvaux, P. FIG. 187.

Petiole 5-50 cm. long, brownish-red to dark brown, the abaxial side rounded; lamina 1-pinnate or bipinnate, ca. 15-50 cm. long, apical pinnules (or apical pinnae of 1-pinnate laminae) reduced to the small, lanceolate terminal segment which is more or less confluent with the lateral segments adjacent to it, rachis of 1-pinnate laminae and pinna-rachises abaxially with pale angles or wings which are irregularly interrupted toward its base, ultimate segments ca. 2 times as long as broad, 5-14 mm. long, firmly herbaceous to chartaceous, the veins usually evident; indusium ca. 0.3 mm. wide, usually repand-erose.

The characters of the pinnae which aid in distinguishing some specimens of this species from some of those of *L. divaricata* are mentioned under that species.

Mexico to Guatemala; Greater Antilles; Guianas to Colombia, south to Bolivia, Brazil.

Open woods, in sandy soil, Loreto and San Martín, 100-800 m.

Specimens seen: LORETO: near Iquitos, *Tryon & Tryon 5180* (BM, F, MO, U, US, USM); Bersalles, prov. Iquitos, *Vargas 11455* (GH). SAN MARTIN: Soritor, *Woytkowski 6247* (US).

6. **Lindsaea stricta** (Sw.) Dryand. Trans. Linn. Soc. 3: 42. 1797.

Petiole ca. 5-80 cm. long, stramineous to pale brown or reddish-brown, the abaxial side rounded; lamina 1-pinnate or bipinnate (rarely to tripinnate), ca. 5-70 cm. long, apical pinnules (or apical pinnae of 1-pinnate laminae) reduced to the small, elliptic-lanceolate to roundish terminal segment which is more or less confluent with the lateral segments adjacent to it, rachis of 1-pinnate laminae and pinna-rachises abaxially rounded to concolorously angled or sulcate, ultimate segments roundish or to 1½ times as long as broad, herbaceous to usually coriaceous, the veins mostly obscure; indusium 0.3-0.5 mm. wide, usually strongly erose to lacerate.

Mexico to Panama; Greater Antilles; Guianas to Colombia, south to Bolivia; Brazil.

In forests, San Martín to Puno, 840-2400 m.

KEY TO VARIETIES

Axes with thick, laterally projecting ridges on the adaxial side, these especially on the upper part of the petiole, on the rachis near the base of the pinnae and at the base of the pinna-rachises. .... 6b. var. *parvula*

Axes lacking such ridges (some intermediates exist). .... 6a var. *stricta*

6a. **Lindsaea stricta var. stricta.** FIG. 188.

Adiantum strictum Sw. Prod. 135. 1788. Type: Jamaica, *Swartz*, S-PA.

Specimens seen: SAN MARTIN: San Roque, *L. Williams 7760* (F, GH); Lamas, *L. Williams 6382* (F, US); near Moyobamba, *Klug 3418* (B, F, G, GH, K, MO, NY, S, US). CUZCO: Beatriz, Maranura, *Bües 894* (US). PUNO: Sandia, *Vargas 11850* (GH).

6b. **Lindsaea stricta var. parvula** (Fée) Kramer, Acta Bot. Neerland. 6: 230. 1957.

Lindsaea parvula Fée, Mém. Fam. Foug. 11: 17. 1866. Type: Trinidad, *Germain;* isotype: P.

Specimen seen: SAN MARTIN: Pascomayo to Moyobamba, *Stübel 1061* (B).

7. **Lindsaea lancea** (L.) Bedd. Ferns Brit. India Suppl. 6. 1876.

Petiole ca. 10-50 cm. long, stramineous to nearly black, the abaxial side with sharp angles or wings, or obtusely angled to rounded in the basal half; lamina 1-pinnate or bipinnate, ca. 5-50 cm. long, apical pinnules (or apical pinnae of 1-pinnate laminae) not or not much reduced, the large or rather large triangular-lanceolate terminal segment free or nearly so from the lateral segments adjacent to it, rachis of 1-pinnate laminae and pinna-rachises abaxially with often pale ridges or wings (the pinna-rachises abaxially rounded at the base), ultimate segments ca. 2 to 3 times as long as broad, 11-45 mm. long, herbaceous, the veins rather evident; indusium 0.2-0.3 mm. wide, entire.

KEY TO VARIETIES

Lamina bipinnate, or 1-pinnate and the terminal segment usually longer than broad, not very asymmetrical, the pinnae ca. 2 to 2½ times as long as broad and the upper ones about half as long as the lower. .... 7a. var. *lancea*

Lamina 1-pinnate, the terminal segment about as long as broad, very asymmetrical, pinnae up to 3 times as long as broad, upper ones little or not reduced (some intermediates exist). .... 7b. var. *falcata*

7a. **Lindsaea lancea var. lancea.** FIG. 189.

Adiantum lancea L. Sp. Pl. ed. 2, 2: 1557. 1763. Type: Surinam, Seba, Thes. 2: t. 64, f. 7, 8 (see Kramer, *op. cit.*).

Lindsaea trapeziformis Dryand. Trans. Linn. Soc. 3: 43. 1797. Type: Grenada, *Smeathman.*

Tropical America.

Dense forest and rocky woods, Amazonas and Loreto to Junín, 100-1600 m.

Specimens seen: AMAZONAS: Campamento, prov. Bagua, *López et al. 4237* (GH). LORETO: near mouth of Río Santiago, *Mexia 6207a* (GH, UC, US); Iquitos, *Killip & Smith 27021* (NY, US). HUANUCO: Tingo María, *Tryon & Tryon 5291, 5296* (BM, F, MO, U, US, USM), *5297* (F, U), *Allard 21209, 21369, 21491* (US). JUNIN: La Merced, *Macbride 5715* (F, US), *Schunke 96* (F), *458* (F, US), *Soukup 1079* (F); Puente Perené, *Coronado 263* (GH, UC); above San Ramón, *Schunke A233* (US), *Killip & Smith 24698* (NY, US); Río Pinedo, n. of La Merced, *Killip & Smith 30676* (US), Santa Rosa, Pichis Trail, *Killip & Smith 26162* (US); Quimiri, Tarma, *Esposto* (USM).

7b. **Lindsaea lancea var falcata** (Dryand.) Rosenst. Hedwigia 46: 79. 1906. FIGS. 182, 190.

Lindsaea falcata Dryand. Trans. Linn. Soc. 3: 41. 1797. Type: French Guiana, *Aublet,* P?

Panama; Guianas to Colombia, south to Bolivia; Brazil.

Forests, Loreto and Junín, 100-1300 m.

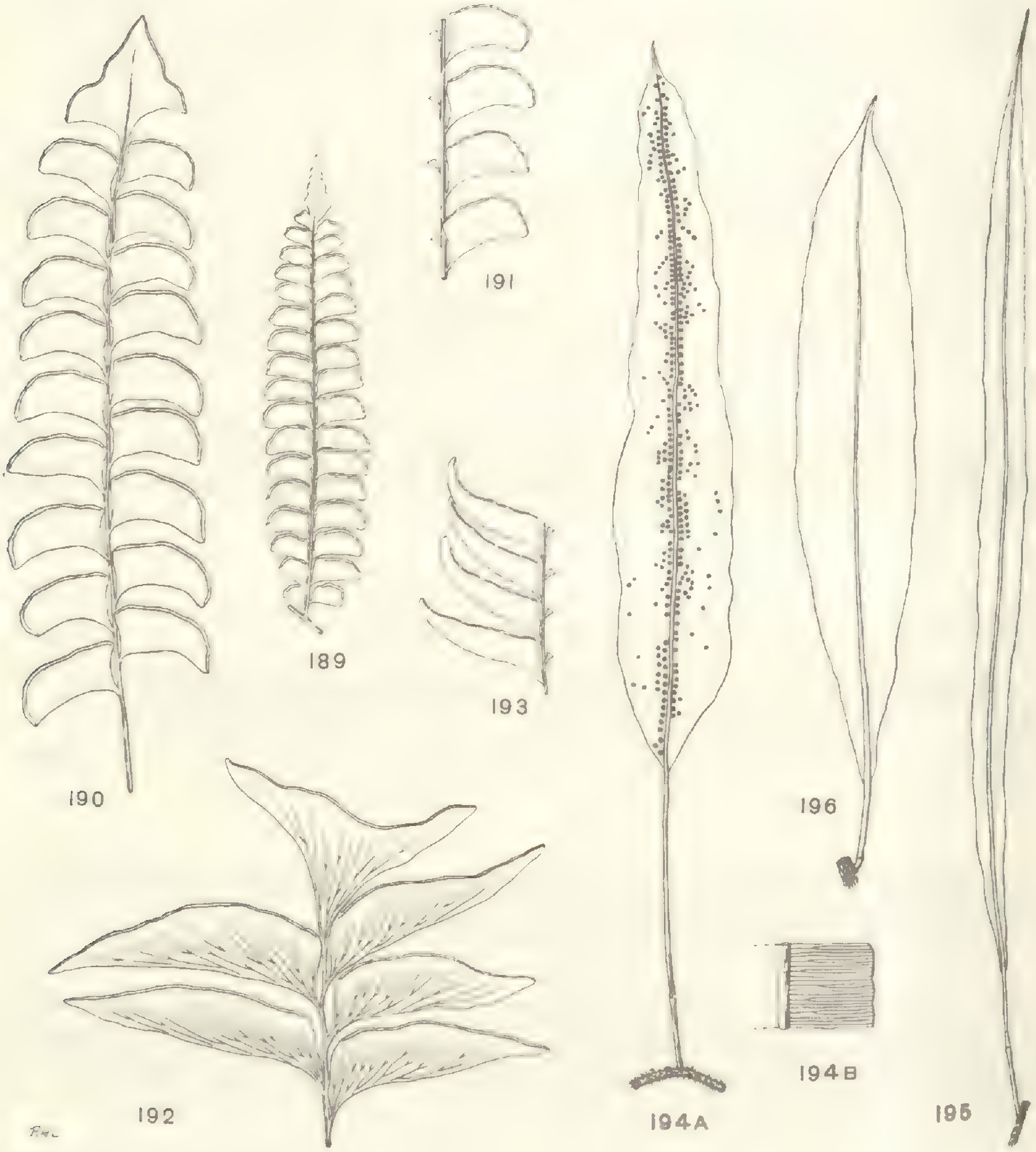
Specimens seen: LORETO: Mishuyacu, near Iquitos, *Klug 379, 1510* (F, NY, US); Timbuchi, alto Río Nanay, *L. Williams 954* (F); Pongo de Manseriche, *Tessmann 4850* (B). JUNIN: La Merced, *Killip & Smith 23966,* in part (F, US).

8. **Lindsaea Schomburgkii** Kl. Linnaea 18: 545. 1845. Type: British Guiana, *Schomburgk 278,* B. FIG. 191.

Petiole 10-35 cm. long, reddish to dark purplish-brown, the abaxial side sharply angled or with protruding paler angles; lamina 1-pinnate, ca. 10-40 cm. long, apical pinnae not or slightly reduced, the large, flabellate terminal segment free, rachis abaxially with often pale angles to sulcate, pinnae ca. 2½ times as long as broad, the largest ca. 20-35 mm. long, firmly herbaceous to coriaceous, veins evident; indusium 0.2 mm. wide, entire to minutely erose-sinuate.

British Guiana, Venezuela, Colombia, Peru and Brazil. In wet, open sand, Loreto and San Martín, 200-1400 m.

Specimens seen: SAN MARTIN: Pajonal, between Río Negro and Rioja, *Stübel 1059* (B); Río Negro, *Woytkowski 6206* (GH). LORETO: Chamicuros (prov. Loreto, dist. Parinari), *Bartlett* (W).



FIGS. 189-196. Fig. 189. *Lindsaea lancea* var. *lancea:* fertile pinna, × ½, Brazil, *Krukoff 7302*, GH. Fig. 190. *L. lancea* var. *falcata:* fertile lamina, × ½, Brazil, *Krukoff 7298*, GH. Fig. 191. *L. Schomburgkii:* central portion of lamina (½), × ½, Brazil, *Spruce 2648*, GH. Fig. 192. *L. latifrons:* apex of fertile lamina, × ½, Peru, *Klug 2890*, GH. Fig. 193. *L. hemiglossa:* portion of fertile lamina (½), × ½, Peru, *Schunke A234*, GH. Fig. 194. *Oleandra articulata:* A, fertile leaf attached to rhizome, × ½, Costa Rica, *Scamman 7600*, GH; B, portion of sterile lamina, × ¾, *idem*. Fig. 195. *O. Lehmannii:* leaf attached to rhizome, × ½, Peru, *Killip & Smith 25870*, GH. Fig. 196. *O. pilosa:* leaf attached to rhizome, × ½, Colombia, *Schultes & Cabrera 14354*, GH.

9. **Lindsaea latifrons** Kramer, Acta Bot. Neerland. 6: 256. 1957. Type: Balsapuerto, Peru, *Klug 2890*, US; isotypes: B, BM, F, G, GH, K, MO, NY, S. FIG. 192.

Petiole 15-45 cm. long, stramineous to pale brown, the abaxial side angled to palely ridged; lamina usually 1-pinnate, rarely bipinnate, ca. 15-40 cm. long, apical pinnae (or apical pinnules in bipinnate laminae) not or slightly reduced, the large, triangular-cuneate to crescent-shaped terminal segment free, rachis and pinna-rachises abaxially angled or palely ridged, ultimate segments 3 to 4 times as long as broad, 6-9 cm. long, firmly herbaceous, the veins evident to obscure; indusium 0.1-0.2 mm. wide, entire.

The next species, *L. hemiglossa*, is closely related to *L. latifrons* and they are both discussed under that species.

Peru.

Dense forest, Loreto, 150-350 m.

Specimens seen: LORETO: Balsapuerto, *Killip & Smith 28596* (US), *28614* (NY, US), *Klug 2890* (B, BM, F, G, GH, MO, NY, S); Tierra Doble, alto Río Nanay, *L. Williams 1068* (F).

10. **Lindsaea hemiglossa** Kramer, Acta Bot. Neerland. 6: 257. 1957. Type: Schunke Hacienda, above San Ramón, Peru, *Schunke A234*, UC; isotypes: GH, US. FIG. 193.

Petiole ca. 10-40 cm. long, stramineous to pale brown, the abaxial side angled to palely ridged; lamina 1-pinnate, ca. 20-40 cm. long, apical pinnae little reduced, the large, triangular-cuneate to crescent-shaped terminal segment free, rachis abaxially ridged, often palely so, ultimate segments 4 to 6 times as long as broad, ca. 4-9 cm. long firmly herbaceous, the veins mostly obscure; indusium ca. 0.1 mm. wide, entire.

When dry, the pinnae of *L. hemiglossa* are usually bright green, while those of the previous species, *L. latifrons*, are dark olivaceous to brown. These two species are represented by few collections and additional materials may indicate that they are variants of a single species.

Ecuador and Peru.

In forests, San Martín and Junín, 1200-1800 m.

Specimens seen: SAN MARTIN: Tarapoto, *Spruce* (K). JUNIN: Chanchamayo, *Schunke 102* (F, US), *511* (F), *806* (F, US); San Ramón, *Killip & Smith 24571* (F, NY, US); La Merced, *Macbride 5624* (F, US); Schunke Hacienda, above San Ramón, *Schunke A234* (GH, UC, US).

TRIBE 11. OLEANDREAE.

34. OLEANDRA Cav. Ann. Hist. Nat. 1: 115. 1799. Type: *Oleandra neriiformis* Cav.

Terrestrial, the rhizome slender, long-creeping or climbing, scaly, bearing the leaves in loose clusters or at wide intervals; leaves small to medium-sized, the lamina simple and entire, glabrous to pubescent, the costa slightly scaly, the petiole articulate at a prominent joint, the portion below the joint (the phyllopodium) short or long, similar to the portion above the joint or scaly like the rhizome, veins free; sori roundish, borne rather irregularly on the veins, not paraphysate, covered by an orbicular to reniform indusium which is attached at the sinus. — 9 species in America.

Maxon, W. R. The American species of Oleandra. Contrib. U. S. Nat. Herb. 17: 392-398. 1914.

The treatment of this genus has been adapted from that of Maxon cited above. Some of the species of *Oleandra* have an erect, short-climbing stem which, with its branches, often produces a shrubby growth. Among the Peruvian species, *O. Lehmannii* and O. *pilosa* have this habit which is unique in this genus. The petiole is articulate, the portion of it below the joint being called the *phyllopodium.*

KEY TO SPECIES

a. Rhizome widely creeping, its scales widely spreading; phyllopodia mostly 5-30 mm. long, slender and naked like the petiole above the joint. .... b.
  b. Lamina and indusia glabrous. .... 1. *O. articulata*
  b. Lamina pubescent, indusia pubescent on the surface, not ciliate on the margin. .... 2. *O. hirta*
a. Rhizome ascending or erect-climbing, its scales closely appressed. .... c.
  c. Lamina glabrous, phyllopodia mostly 10-20 mm. long, slender and naked like the petiole above the joint, indusium glabrous. .... 3. *O. Lehmannii*
  c. Lamina pubescent, at least in part, phyllopodia 1-3 (-5) mm. long, stout and at first scaly like the rhizome, indusium pubescent on the surface and with ciliate margins. .... 4. *O. pilosa*

1. **Oleandra articulata** (Sw.) Presl, Tent. Pterid. 78. 1836. FIG. 194.

Aspidium articulatum Sw. Jour. Bot. Schrad. 1800(2): 30. 1801. Type: Martinique, Plumier, Fil. t. 136 (See Maxon, Contrib. U. S. Nat. Herb. 17: 394, for a discussion of the choice of the type and the correct application of the name).

Aspidium nodosum Willd. Sp. Pl. 5: 211. 1810, *(nom. superfl., illegit.)*. Type: the same as that of *Aspidium articulatum* Sw.
Oleandra nodosa (Willd.) Presl, Tent. Pterid. 78. 1836, (*illegit.*)

Rhizome widely creeping, scales spreading; phyllopodia ca. 5-30 mm. long, slender, without scales; lamina glabrous, ca. 10-35 cm. long, about 1/4th to 1/10th as broad, caudate to rather abruptly acute at the apex, gradually narrowed to usually broadly cuneate, rarely subcordate at the base; indusium glabrous.

The costal scales of this widely distributed species are most commonly ovate-deltoid to long-deltoid and acuminate. The Peru and Bolivian material I have seen has them subulate to narrowly lanceolate and acuminate. Scales of the same shape, however, occur in other parts of the range of *O. articulata*, either by themselves, or mixed with the more common kind; there is no evidence that the variation has taxonomic importance.

Tropical America.

Dense forest, Junín, 1400-1900 m.

Specimens seen: JUNIN: Eneñas, Pichis Trail, *Killip & Smith 25756* (F, NY, US); Schunke Hacienda, above San Ramón, *Killip & Smith 24878* (NY, US).

2. **Oleandra hirta** Brack. in Wilkes, U. S. Expl. Exped. 16: 214, Atlas t. 29. 1854. Type: Organ Mountains, Brazil, *Brackenridge*, US!

Rhizome widely creeping, scales spreading; phyllopodia ca. 5-30 mm. long, slender, without scales; lamina pubescent, ca. 10-20 cm. long, about 1/5th as broad, caudate to abruptly acute at the apex, narrowly to broadly cuneate at the base; indusium pubescent on the surface, glabrous on the margin.

This species is not known from Peru but I have seen a specimen from Bolivia *(Tate 1152,* NY) and it may well be discovered in Puno or Cuzco.

Brazil, Venezuela and Bolivia.

3. **Oleandra Lehmannii** Maxon, Contrib. U. S. Nat. Herb. 17: 395. 1914. Type: Colombia, *Lehmann XLII*, US! FIG. 195.

Rhizome ascending or erect and climbing, scales closely appressed; phyllopodia ca. 10-20 mm. long, slender, without scales; lamina glabrous, ca. 15-25 cm. long, about 1/20th as broad, gradually tapered at apex and base; indusium glabrous.

The earlier name, *Oleandra micans* Kze., discussed under *O. pilosa,* may apply to this species.

Venezuela and Colombia to Peru.

Dense forest, Junín, 1800 m.

Specimens seen: JUNIN: Dos de Mayo, Pichis Trail, *Killip & Smith 25870* (F, GH, NY, US).

4. **Oleandra pilosa** Hook. Gen. Fil. t. 45 B & text. 1840 Type: Berbice, British Guiana, *Schomburgk 416,* K! FIG. 196.

Aspidium pendulum Splitg. Tijds. Nat. Gesch. 7: 412. 1840, not Raddi, 1819. Syntypes: Surinam, *Splitgerber;* British Guiana, *Schomburgk 416;* isotype: K!

Rhizome ascending or erect and climbing, scales closely appressed; phyllopodia 1-3 (to rarely 5) mm. long, stout, at first scaly like the rhizome; lamina pubescent, sometimes sparingly so, ca. 10-35 cm. long, about 1/5th to 1/10th as broad, caudate, acuminate or acute at the apex, gradually narrowed to rather rounded at the base; indusium pubescent on the surface and with a ciliate margin.

The pubescence on the lamina is variable in its distribution. Most specimens are somewhat pubescent on all parts but others may be partially glabrous, especially on the leaf tissue beneath.

Oleandra micans Kze. Bot. Zeit. 1851 : 346. (Type: Huallaga superior, Peru, 1830, *Poeppig, (Diar. 1958),* LZ, destroyed) may be a synonym of this species, or it might be an earlier name for *O. Lehmannii.* The description mentions only one character of value in establishing the identity of the name and that is "caudice . . . adpresse paleaceo . . ." but this serves only to place it in the general alliance of *O. pilosa.*

Guianas to Colombia, south to Bolivia.

In dense forest, Huánuco to Puno, 600-1300 m.

Specimens seen: HUANUCO: Tingo María, *Allard 21215, 21999* (GH, US). CUZCO: Río Marcapata, *de Lantreppe* (NY); San Pedro, prov. Paucartambo, *Vargas 6801* (UC, US). PUNO: Tatanara, *Lechler 2539* (B, K).

INDEX TO NAMES

Accepted names are in roman type, synonyms are in italic

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EVOLUTION OF SELF-COMPATIBILITY AND RACIAL DIFFERENTIATION IN LEAVENWORTHIA (CRUCIFERAE)

DAVID G. LLOYD[1]

Charles Darwin (*e.g.*, 1876) showed that, in the majority of plant species he studied, progeny from crossing two plants are usually superior to those resulting from self-fertilization, and that many plant species have devices which ensure that the flowers are not regularly self-fertilized. In the century since Darwin's work, it has become apparent that one of the commonest means whereby angiosperm species restrict self-fertilization is through the operation of self-incompatibility systems. Self-incompatible species have been found in at least 78 families and occur in every major phylogenetic line (Pandey, 1960). Brewbaker and Majumder (1961) estimate, from a compilation by Fryxell (1957), that approximately 250 of 600 genera studied contain one or more self-incompatible species.

Many genera contain both self-incompatible and self-compatible species (Fryxell, 1957; Stebbins, 1957). Within the *Cruciferae*, of 182 species studied, 80 are self-incompatible and 102 are self-compatible, and many genera contain both self-incompatible and self-compatible species (Bateman, 1955). A change from self-incompatibility to self-compatibility, or vice versa, has apparently occurred many times. The majority of recent authors (*e.g.*, Mather, 1943a; Crowe, 1964) believe that the change has been from self-incompatibility to self-compatibility in most, if not all, cases where multi-allelic systems are involved.

In many genera, the self-incompatible species have adaptations to insect pollinations such as nectaries and conspicuous flowers, whereas the self-compatible species have partially or completely lost these adaptations and have evolved devices to ensure the success of self-pollination. In addition, the acquisition of self-compatibility may have secondary effects on the distribution, variation, and evolutionary potential of such species. It is often said that self-

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compatible species are able to adapt more closely to the environment in which they live, but have a reduced genetic variability and a more limited evolutionary potential. In some groups too, self-compatible species are more widely distributed than their self-incompatible relatives (Baker, 1953).

This has led to considerable speculation on the selective advantage of the change in the breeding system. The nineteenth century naturalists observed that self-fertile species are more common at high altitudes and high latitudes in Europe, and that many of these species have devices to ensure self-pollination if cross-pollination fails; they believed that self-fertilization enabled a plant to set sufficient seed when unfavorable weather conditions or a lack of insect visitors restricted cross-pollination. Since the development of the theory of genetic systems (Darlington, 1939; Mather, 1943a) this explanation has been used less, and many authors have placed more emphasis on the apparent ability of self-compatible races to adapt more closely to their immediate environment.

Rollins (1963) has recently given an account of the systematics and evolution of *Leavenworthia*, which includes a description of the evolution of self-compatibility and associated morphological characters in certain populations of *L. alabamica* and *L. crassa* and at least two other phyletic lines in the genus. The existence in both *Leavenworthia crassa* Rollins and *L. alabamica* Rollins of self-incompatible and self-compatible geographical races in a very small area of northwest Alabama (Rollins, 1963) suggests that the change in the breeding system has occurred recently in these species. Both species therefore offered an exceptional opportunity to study the factors influencing the evolution of self-compatibility and the effects of the change in the breeding system on the morphology and distribution of the self-compatible populations.

The present study on *L. crassa* and *L. alabamica* has revealed a much more complicated pattern of geographical variation, largely associated with the evolution of self-compatibility, than was previously known. Fifteen geographic races of *L. crassa* and four geographic races of *L. alabamica* were distinguished amongst the populations grown in a greenhouse, and these are informally described below. The self-compatible races differ in the degree to which they have lost adaptations for insect pollination and have gained structural devices which increase the efficiency of self-pollination. The morphology, ecology and distribution of the self-incompatible and self-compatible races of *L. crassa* and *L. alabamica* have been studied in detail, and factors affecting the number of insect visitors in the natural habitat of *Leavenworthia* have been examined.

GENERAL METHODS

The projects reported in this study were done on plants growing in nature and on plants grown in a greenhouse in Cambridge, Massachusetts, from seeds collected in nature. Wherever possible measurements were made on both material collected in nature and on material grown in the greenhouse under relatively uniform conditions.

L. crassa and *L. alabamica* are winter annuals endemic to northwest Alabama. The seeds germinate in the fall, and the plants grow slowly throughout the winter and flower from approximately March 10 to April 20 or later, depending upon how rapidly the spring rains diminish and the temperature increases. The fruits mature and the seeds are shed at the end of April and beginning of May.

Field studies were conducted in the flowering seasons of 1961, 1962 and 1964. Thirteen of the nineteen races of *L. crassa* and *L. alabamica* described below are restricted to a small area approximately 4½ miles (from west to east) by 4 miles (from south to north) near Massey[1], Morgan county, Alabama (map 1). This area, referred to henceforth as the Massey-Lebanon district, was searched and studied more intensively than the areas to the west, where the remaining races of *L. crassa* and *L. alabamica* are scattered over a much larger area.

The greenhouse material was grown in two lots, from November 1961 to March 1962, and from January to June 1963. These two plantings are referred to as the 1962 and 1963 greenhouse material, respectively. The 1962 material

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[1] The small village of Massey is the same as that referred to as McKendry by Rollins (1963); the name has recently been changed.

included plants from 13 populations belonging to seven races of *L. crassa* and three races of *L. alabamica.* The 1963 material included plants from 30 populations from all of the described races of both species.

The seeds were germinated in a layer of peat moss over soil in three inch clay pots, and the seedlings were transplanted to three inch pots, and later to four inch pots as their growth required it. Despite extreme care considerable difficulty was experienced in growing the plants, and many plants, particularly of the 1963 material, became unhealthy in the later stages of flowering. Only plants on which less than five per cent of the flowers were abnormally arrested in their development were measured; these were considered to be reasonably representative of growth under conditions which were relatively uniform and close to optimal for the greater part of the lives of the plants.

The races were recognized on the basis of differences expressed in the greenhouse. A number of measurements were made on the plants of each population grown in the greenhouse, and features distinguishing the races were noted. Many of the races are not distinguishable under natural conditions, and several of the races were not even suspected of being distinct until they were grown in 1963. The identification of populations which were not grown in the greenhouse is based on observations and measurements made in the field in 1962. In some cases the racial identity of these populations is tentative: it is quite possible that additional races might be distinguished if more populations were grown in a greenhouse. The two westernmost races of *L. alabamica* have not been grown in the greenhouse — see undescribed races of *L. alabamica* below.

Voucher specimens of plants collected in nature from one or more populations of each race of *L. crassa* and *L. alabamica*, and of one plant of every population grown in the greenhouse in 1963, have been deposited in the Gray Herbarium of Harvard University. Insects collected on *Leavenworthia* flowers have been placed in the Museum of Comparative Zoology, Harvard. Negatives of photographs of young plants, flowering plants, leaves, flowers and fruits of all the described races of *L. crassa* and *L. alabamica* have been deposited in the negative collection of the Gray Herbarium.

THE RELATIONSHIPS BETWEEN L. ALABAMICA, L. CRASSA AND OTHER SPECIES OF LEAVENWORTHIA

Leavenworthia is a small, well-defined and isolated genus of the *Cruciferae* confined to the southeastern United States. The genus most closely related to *Leavenworthia* is possibly *Selenia* Nutt., but the relationship is not close (Rollins, 1963).

All of the species are highly specialized in their ecological requirements; they are winter annuals whose natural habitat is confined to limestone, dolomitic limestone or dolomite outcrops with shallow soils unable to support forest but with sufficient moisture in the fall and spring to enable the *Leavenworthia* plants to complete their reproductive cycle (Quaterman, 1950; Rollins, 1963). These areas are known as cedar glades, since the dominant tree surrounding them is the 'red cedar', *Juniperus virginiana* L.

Amongst the seven species of *Leavenworthia* there are three basic chromosome numbers, n=11, 15 and 24 (Rollins, 1963). Each chromosome level has probably been attained only once by the living species, so that species with the same chromosome number represent natural groups within the genus.

Three species, *L. stylosa* Gray, *L. torulosa* Gray and *L. uniflora* (Michx.) Britton, have n=15 chromosomes. The center of distribution of these three species (and of the genus as a whole) is the Central Basin of Tennessee. Within the Central Basin these three species are sympatric and often grow intermingled amongst each other. *Leavenworthia stylosa*, the most primitive species of the three, is self-incompatible throughout its range and is wholly confined to the Central Basin. *Leavenworthia torulosa* is self-compatible and has lost many of the adaptations to insect pollination: it has a wider range than *L. stylosa* in Tennessee and also occurs in southern Kentucky. *Leavenworthia uniflora*, the most highly autogamous species in the genus, also has the widest distribution of all *Leavenworthia* species.

The species at the n=15 chromosome level have thus become secondarily sympatric after their prior speciation in geographic isolation. The reproductive isolating mechanisms between them are complete — no hybrids have ever been found in nature, and the species cannot be artificially crossed (Rollins, 1963).

The three species with 11 chromosome pairs, *L. alabamica*, *L. crassa* and *L. exigua* Rollins, offer a strong contrast to the species with 15 chromosome pairs in the pattern of distribution and in the hybridization of the species. The glade populations of these species are completely allopatric, although the distribution of the races of *L. alabamica* and *L. crassa* is very complicated. *L. exigua* is the most advanced species in this group in regard to its breeding system: all of the populations tested are self-compatible, and have to a large extent lost the ancestral adaptations to cross-pollination by insects, such as large flowers and a noticeable odor (Rollins, 1963). *Leavenworthia exigua* is also the most widespread of the species with 11 chromosome pairs, occurring in the Central Basin, northwest Georgia, central Alabama and north Kentucky. *Leavenworthia exigua* is less closely related to *L. crassa* and *L. alabamica* than the latter species are to each other, and it cannot be crossed with either *L. crassa* or *L. alabamica* (Rollins, 1963).

Leavenworthia crassa and *L. alabamica* are clearly the two most closely related species in the genus. They differ only in several silique characters. The siliques of *L. crassa* never exceed 13 mm in length and are fleshy, whereas the siliques of all races of *L. alabamica* exceed 17 mm in length under favorable conditions and are not fleshy. The number of seeds in each silique depends upon the environmental conditions and varies between the races in both species, but there are often more than twelve seeds per silique in *L. alabamica*, and usually less than ten seeds per silique in *L. crassa*. In addition adjacent seeds in each locule usually overlap in *L. crassa*, but in *L. alabamica* the seeds in each locule are well spaced, or barely touching (fig. 5).

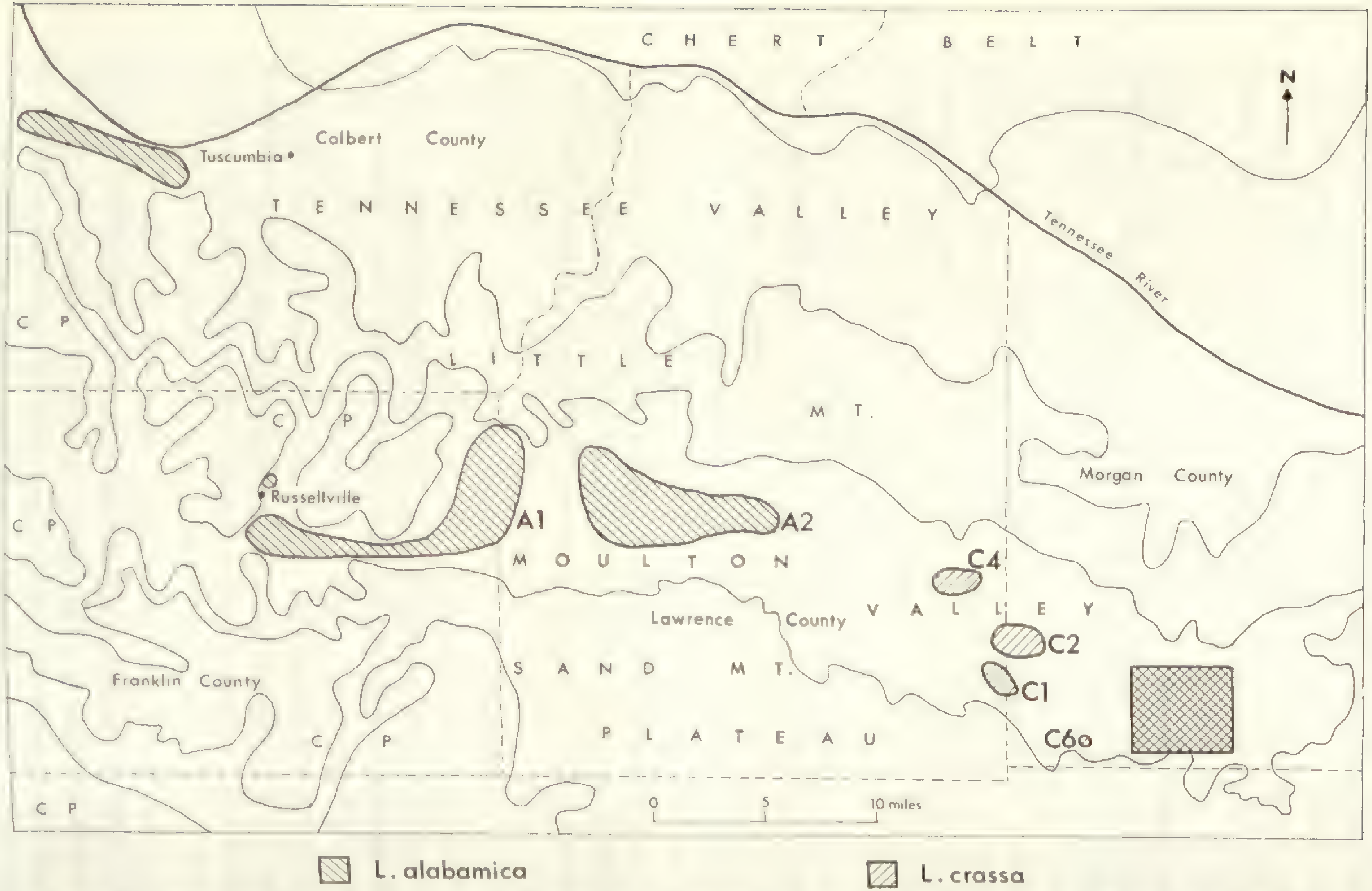
Apart from these fruit characters there are no constant differences between the two species, and the self-incompatible races of *L. crassa* and *L. alabamica* are otherwise almost identical. The close relationship between *L. crassa* and *L. alabamica* is also shown by the fact that they hybridize easily on cultivated fields where they have met, and under experimental conditions, to produce vigorous and fertile offspring (Rollins, 1963).

The siliques of *L. crassa* are the most distinct of any species in the genus. All other species have much longer siliques in which the seeds are well spaced, as in *L. alabamica.* Indeed, *L. alabamica* was at first confused with both *L. stylosa* and *L. aurea* and was not separated from *L. stylosa* until very recently (Rollins, 1963). It seems probable that the unique silique characters of *L. crassa* are derived and have arisen in the relatively recent divergence of *L. crassa* from *L. alabamica.*

The geographical distribution of *L. crassa* and *L. alabamica* provides some additional evidence that *L. crassa* has diverged only recently from a self-incompatible ancestor of *L. alabamica*, perhaps within a few miles of its present very restricted distribution (the most distantly separated glade sites of *L. crassa* are only 11 miles apart). *Leavenworthia crassa* is confined to southeast Lawrence Co. and southwest Morgan Co., in the Moulton Valley of northwest Alabama (map 1).

Leavenworthia alabamica has a somewhat wider distribution than *L. crassa*, although the most distantly separated glade sites of *L. alabamica* are only about 62 miles apart. Populations of *L. alabamica* occur at the western end of the Moulton Valley in Franklin County and the adjacent western half of Lawrence County, and at the eastern end of the Moulton Valley in southwest Morgan Co. In addition there are several populations in the Tennessee Valley (Colbert Co.).

The two species do not occur anywhere in the same glade although the distribution of *L. crassa* lies entirely within that of *L. alabamica*, and within the Massey-Lebanon district of Morgan County the glade populations of *L. crassa* are almost entirely surrounded by those of *L. alabamica.* Apparently both species have migrated slowly over the Moulton Valley as suitable cedar glades have shifted in position. It is remarkable that the two species have not met in any of the present glades, and it seems unlikely that both *L. crassa* and *L. alabamica* could have migrated into the Moulton Valley region and have maintained their identity in close proximity during a long period of slow wanderings around the valley. I believe instead that *L. crassa* diverged from *L. alabamica* after the ancestors of the two species reached the Moulton Valley, and perhaps after *L. alabamica* had spread throughout the length of the valley that it presently occupies.



Map 1. Distribution of *L. alabamica* and *L. crassa* in northwest Alabama. Each hatched area is occupied by the race indicated beside it. The cross-hatched area, the 'Massey-Lebanon district' contains 11 races of *L. crassa* and 2 races of *L. alabamica* (see maps 2 to 5). The physiographic provinces are drawn from Harper (1942, Fig. 1). C.P. = Coastal Plain (Cretaceous).

One species of *Leavenworthia*, *L. aurea* Torrey, has 24 pairs of chromosomes; it is a self-compatible polyploid most closely related to *L. exigua* and *L. alabamica* (Rollins, 1963). *L. aurea* has a disjunct distribution in Oklahoma and Texas, completely outside the range of the other species of the genus.

The species of *Leavenworthia* are thus spread over a considerable number of discontinuous areas in ten states. *Leavenworthia* has extremely limited powers of dispersal (see below) and it is highly probable that members of the genus must once have occurred in the intervening areas between those presently occupied. Moreover, the widely different diploid chromosome numbers (n=11 and n=15) and the isolated polyploid, *L. aurea* (n=24), which cannot be derived directly from the existing diploid chromosome numbers, indicate that *Leavenworthia* has previously evolved forms which are now extinct. It is thus impossible to trace the full history of speciation and migration in the genus.

Nevertheless, from the distribution of the species of *Leavenworthia* and of other cedar glade plants one can make certain suggestions concerning the geographical and evolutionary history of the ancestors of *L. crassa* and *L. alabamica*. The most important question in this regard is whether the common ancestor of *L. crassa* and *L. alabamica* diverged from the other species in Alabama or whether it reached the area secondarily and became extinct elsewhere. I believe that several lines of evidence indicate that the ancestor of *L. alabamica* and *L. crassa*, (and, independently, *L. exigua* and *L. uniflora*) migrated into Alabama from the north.

The area occupied by *Leavenworthia* can be broadly divided into a western and an eastern section. The western section in Missouri, Arkansas, Oklahoma and Texas occurs within the Interior Highlands, except for the populations of *L. aurea* in Texas, which are in the Coastal Plain Province (Fenneman, 1938). The western section is occupied only by *L. uniflora* (n=15) and *L. aurea* (n=24). The species in the eastern section from Ohio and Indiana to Alabama and Georgia occur mostly in the Interior Low Province, with peripheral populations of *L. exigua*, *L. torulosa* and *L. uniflora* in the Appalachian Plateau Province. All of the species except *L. aurea* occur in the eastern section. The eastern and western sections are at present separated from each other by the Mississippi Alluvial Plain which is generally quite unsuitable for occupation by *Leavenworthia.*

Steyermark (1934) has pointed out that a number of other plants have disjunct distributions similar to that of the genus *Leavenworthia,* with populations in the Interior Highlands and others in the southern Appalachian Plateau and adjacent areas. Braun (1950) states that the Tertiary connections between the Appalachian and Interior Highlands, *northward* around the Mississippi Embayment have been of fundamental importance in vegetational development. It seems likely that this was also the route taken by *Leavenworthia* in migrations between the Appalachian and Interior Highlands. There is no conclusive evidence to suggest whether *Leavenworthia* originated in the western or eastern sections of the area it occupies at present. The resemblance between the flora of the cedar glades and that of the prairies of the Great Plains (Harper, 1926; Erickson *et al.,* 1942) perhaps suggests a western origin for *Leavenworthia.*

If *Leavenworthia* has indeed come into the Interior Highlands from the west by a northern route, the species must have come into Alabama from the north. *Leavenworthia exigua* at present occurs from northern Kentucky to central Alabama, and it is striking that the most primitive (least adapted to autogamy) variety, var. *laciniata,* is in Kentucky, and the most advanced variety, var *lutea,* occurs in Alabama. This perhaps suggests a southward migration by *L. exigua.*

A second and more important line of evidence lies in the nature of the cedar glades in Tennessee and Alabama. Many authors have stressed that the cedar glades are most extensive and characteristic in the Central Basin, where they are typically developed on thin-bedded Lebanon limestone of Ordovician age. This formation frequently weathers to form large areas of denuded outcrops with low relief — the sites of the cedar glades. Quaterman (1950) estimated that there are approximately 300 square miles (5 to 6 per cent of the Central Basin) of rocky barren flats supporting cedar glade growth in central Tennessee.

The cedar glades of northern Alabama are much smaller than those of the Central Basin. The Bangor and Tuscumbia limestones of Mississippian age on which they occur are predominantly massive to thick-bedded. These limestones form much smaller areas of denuded outcrops, mostly on mountain slopes (Harper, 1926; Johnston, 1930). Harper did not even recognize these areas as cedar glades, though it is apparent from their species composition that they resemble the cedar glades of the Central Basin more closely than they do any other habitat (Harper, 1926; Braun, 1950). The suitable limestone formations in northern Alabama are sandwiched between younger and older non-calcareous rocks, whereas the entire Central Basin is calcareous. The cedar glades of Alabama have probably always been small and widely scattered, although in past times they have undoubtedly occurred in places different from those they occupy now.

The cedar glades of Alabama are not only geologically and ecologically marginal; they are geographically peripheral too. They occur mostly on the southern margin of the Highland Rim section of the Interior Low Plateau. To the west, south, and east of northwestern Alabama the Paleozoic limestones are largely covered by younger non-calcareous sediments of the coastal plain and the Appalachian Highlands. North of Alabama, however, calcareous formations have been extensively developed for a long time and could well have provided a source for the population of the cedar glades of Alabama.

The geological nature of the Interior Low Plateau suggests that the Paleozoic limestones of the area were exposed in the Central Basin of Tennessee earlier than in Alabama. The Nashville Dome is the major structural feature of the present topography and geology of the Interior Low Plateau. The crest of this dome is in central Tennessee. As this dome rose, the sediments above the Paleozoic formations were eroded away and the Paleozoic sediments were exposed. "That the Ordovician rocks in Limestone County [Alabama] and in Tennessee to the north were exposed prior to the exposure of Mississippian strata south of the Tennessee River is entirely probable owing to the greater amount of uplift in the proximity of the crest of the dome" (C. W. Copeland, pers. comm.).

If the limestone areas occupied by *Leavenworthia* were

FIG. 1. (above) Photograph of a medium-sized cedar glade occupied by plants of race a1 *(L. alabamica)*.

FIG. 2. (below) Photograph of plants of race a1 *(L. alabamica)* growing in a cedar glade.

exposed in Tennessee before being exposed in Alabama it is more likely that the species of *Leavenworthia* have migrated into Alabama from Tennessee, and not vice versa. According to this hypothesis, the common ancestor of *L. alabamica* and *L. crassa* formerly existed in Tennessee, then migrated to Alabama, and subsequently became extinct except in Alabama. A similar migration was proposed by Baldwin (1943) to account for the distribution of *Sedum pulchellum* Michx. Baldwin believes that the Central Basin has been the center of variability and dispersal of the polyploid series within *Sedum pulchellum*. From the Central Basin the diploid form has succeeded in extending itself to the south and west (including Lauderdale and Madison Counties, Alabama) and the tetraploids have extended beyond the Central Basin to the north.

THE DESCRIPTION OF L. CRASSA, L. ALABAMICA AND THEIR RACES

As described previously, *L. crassa* and *L. alabamica* are closely related species with the same chromosome number (n=11), differing in only a few silique characters. Within *L. crassa*, fifteen distinguishable races have been recognized from field and greenhouse studies. Within *L. alabamica* four races have been recognized amongst populations grown in the greenhouse; two additional races seen in the field have not been studied in detail. Since the species have been previously described (Rollins, 1963) and the races are not being formally recognized, both the species and races are given only informal descriptions below.

The descriptions of the species and races are all based on observations on plants growing in nature, and on plants grown in a greenhouse in the winters of 1962 and 1963. All of the races which have been recognized were grown during 1963, and their separation is based primarily on data collected then. The measurements given in the descriptions below will all be discussed later and are averages obtained on the 1963 greenhouse material with the following exceptions:

1. The flower colors given are those present in populations growing in the wild.
2. The fraction of positive results in self-pollination trials

is based on the combined averages of all tests made on the populations of each race, as described below.

3. The lengths of the siliques (excluding styles) are those of the largest fruit of any population of each race, from collections of plants growing in the wild in 1962 and in the greenhouse in 1962 and 1963. The 1963 greenhouse material alone could not be used, since some of the plants grown then became unhealthy later in the flowering period, and many of the fruits did not mature properly.

Planar shapes are described on the system published by the Systematics Association Committee for Descriptive Biological Terminology (1962).

To simplify the descriptions of *L. crassa, L. alabamica* and their races, a combined description of *L. crassa* and *L. alabamica* (including the differences between the species) is given first. This is followed by descriptions of the races of *L. crassa* and *L. alabamica,* which mention only the distinguishing features of each race, including measurements.

In the following combined description of *L. crassa* and *L. alabamica,* characters which differ consistently between the species and characters which are shared by all races of both species are given in Roman type. Characters which vary between races of either species are given in italics; the expression given for each of these characters is that prevailing in most races of both species. Measurements given in italics are those of the lowest and highest racial averages amongst the races of *L. crassa* and *L. alabamica,* except for the silique lengths which show the range in the longest measurement obtained in each race.

A COMBINED DESCRIPTION OF L. CRASSA AND L. ALABAMICA

The plants are herbaceous glabrous winter-annuals. Under poor conditions in nature they produce a few small, simple and entire leaves in a basal rosette, and one or a few flowers borne singly on erect scapes originating at the center of the rosette. Under more favorable conditions in nature and the greenhouse the plants bear thirty or more basal leaves, many scapose flowers and up to fifteen branches, each bearing one or a few leaves, then many flowers in a raceme. The later basal leaves are lyrately pinnatifid, *when mature are straight, raised off the ground, and more than 8 mm long. The terminal lobes are flat, circular, and sinuate to shallowly crenate; the apices of the crenations are acute to obtuse, but not apiculate or mucronate; the apices of the terminal lobes are rounded; the bases of the terminal lobes are variable (cordate to obtuse).* The lateral lobes are always variable in shape, *with irregularly scattered anthocyanin spots on the upper surface.*

The branches average 4.1 to 29.3 cm long, are initially suberect, and later extend beyond the scapes of the central flowers, becoming procumbent.

The petals average 7.81 to 12.07 mm long and consist of a narrow proximal claw parallel to the axis of the flower and a broader distal limb. *The petal limbs are broadly obovate,* emarginate *(emarginations average 0.35 to 1.09 mm deep), and bend outwards at right angles to the claw in fully open flowers. The petals open at the same time as the sepals and close again to a vertical position.* At the base of each petal limb are three nectar-guides radiating from the middle of the petal towards the distal end of the limb. The nectar guides are composed of superimposed brown and orange pigments; *the orange pigment predominates: the lateral nectar-guides are only slightly shorter than the central one.* Apart from the nectar-guides which are always present, the following petal color patterns have been recognized (the first two are by far the most common): a. 'Yellow': a yellow pigment is uniformly present over the petal limbs. b. 'Yellow-centered': the proximal portion of the petal limbs is yellow, and the distal portion is white; *the yellow portion occupies half, or less, of the limbs.* The yellow portion ends abruptly, *is conspicuous and contrasts strongly with the white portion,* and the flowers thus have a yellow 'eye' surrounded by the white portions of the petals. c. 'orange-centered': as for yellow-centered, except that the proximal portion of the petal limbs is orange. d. 'Imperfect-centered': the proximal portion of the petal limbs is yellow and does not end abruptly, but blends into the distal white portion, and is longer than in yellow-centered flowers, particularly towards the petal margins. Other patterns occur rarely but are of little importance. In nature yellow-centered and orange-centered flowers may have visible anthocyanin on the undersides of the petal limbs. *Under greenhouse conditions the petals are without visible anthocyanin. The flower color patterns present in nature are described separately under each race.*

The stamens are strongly tetradynamous. The anthers of single stamens are always introrse and are approximately level with the petal claws. The anthers of the paired stamens are approximately at the level of the stigma, *beyond the plane of the petal limbs, close together around the stigma, and extrorse after the filaments have turned 135 to 180° (figs. 3 and 6). The pollen:ovule index (the average number of pollen grains per flower divided by the average number of ovules per flower) averages between 2770 and 9100.*

The pistils (ovary plus style) extend to or beyond the top of the petal claws, *and average from 4.23 to 6.90 mm long.* In open flowers of *L. crassa* the ovary is globose to ovoid and shorter (2.3 mm or less) than the style, *which averages 2.2 to 4.6 mm.* In open flowers of *L. alabamica* the ovary is flattened and longer (ca. 3 mm) than the style, *which averages 2.0 to 2.7 mm.*

The mature siliques (excluding styles) of *L. crassa* are fleshy and terete (2.5 to 5.0 mm thick); *the septa are oblong to broadly elliptic and average 8.8 to 14.8 mm long, with a rectilinear to round apex.* The mature siliques of *L. alabamica* are not fleshy and flattened (1.5 to 2.5 mm thick); *the septa are narrow-oblong to oblong, and average 17.6 to 27.9 mm long with an acute to obtuse apex. In both species the septa of mature siliques sometimes have one (or occasionally more) small holes near the base.*

The seeds are flattened, winged, circular to broadly elliptic and ca. 3 mm wide. The seeds in each locule partly overlap in *L. crassa*, but are usually entirely separated in *L. alabamica* (fig. 5).

Some races are self-incompatible (with varying frequencies of pseudo-compatibility); other races are self-compatible; the fraction of positive results on self-pollination averages between 0.17 and 1.00. The fraction of flowers which set seed spontaneously in the greenhouse (are auto-fertilized) averages between 0.01 and 0.30. The advancement indices of the races range from 0 to 100.

It is apparent from maps 1 to 5 and the following discussions that the distinguishable racial entities are all allopatric geographical races. But since the distribution pattern is very complex and concentrated in a small area, and the differences between races are minor and not always apparent in nature, I believe that it is not advisable to give these races any formal taxonomic recognition.

A limited number of crosses between the races has been made. Within *L. crassa*, the ten attempted inter-racial combinations were all successful, and within *L. alabamica* the two attempted inter-racial combinations were successful (Lloyd, unpublished). Crosses between self-incompatible and self-compatible races, however, give a lower seed set when the self-compatible race is used as the male parent, indicating the development of incipient reproductive isolating mechanisms. There is also a possibility that one or more of the races of *L. crassa* and *L. alabamica* may have chromosome numbers other than the n=11 found in the populations studied by Rollins (1963). However, no chromosome counts were made in the present study. The counts made by Rollins were on the races designated as c1, c2, c5, c7 and c15 *(L. crassa)* and a1, a2, and a4 *(L. alabamica)* below, and included the most primitive and most advanced race in both species. There is therefore no evidence at present that any of the racial entities described below deserve specific recognition.

In the following sections it will be shown that the loss of self-incompatibility in some of the races of *L. crassa* and

L. alabamica has been accompanied by a whole complex of associated changes in other characters. These changes, and other differences which are not related to the change in the breeding system, provide the distinguishing features of the races of the two species.

The races of *L. crassa* and *L. alabamica* are designated by the first letter of the species to which they belong, followed by a number indicating their rank within the species in the order of increasing advancement indices. The advancement indices, described on page 70, indicate how far each race has evolved in the trends in ten characters associated with the evolution of self-compatibility. The evolution of these characters, including self-compatibility itself, is discussed in detail after the race descriptions. The description of a race as primitive or advanced refers only to its position in regard to the characters associated with the evolution of self-compatibility.

The two intraspecific categories described by Rollins (1963), *L. crassa* var. *elongata* and *L. alabamica* var. *brachystyla* are the most advanced of the recognized races in their respective species. *Leavenworthia crassa* var. *elongata* is therefore designated as race c15 and *L. alabamica* var. *brachystyla* is designated as race a4.

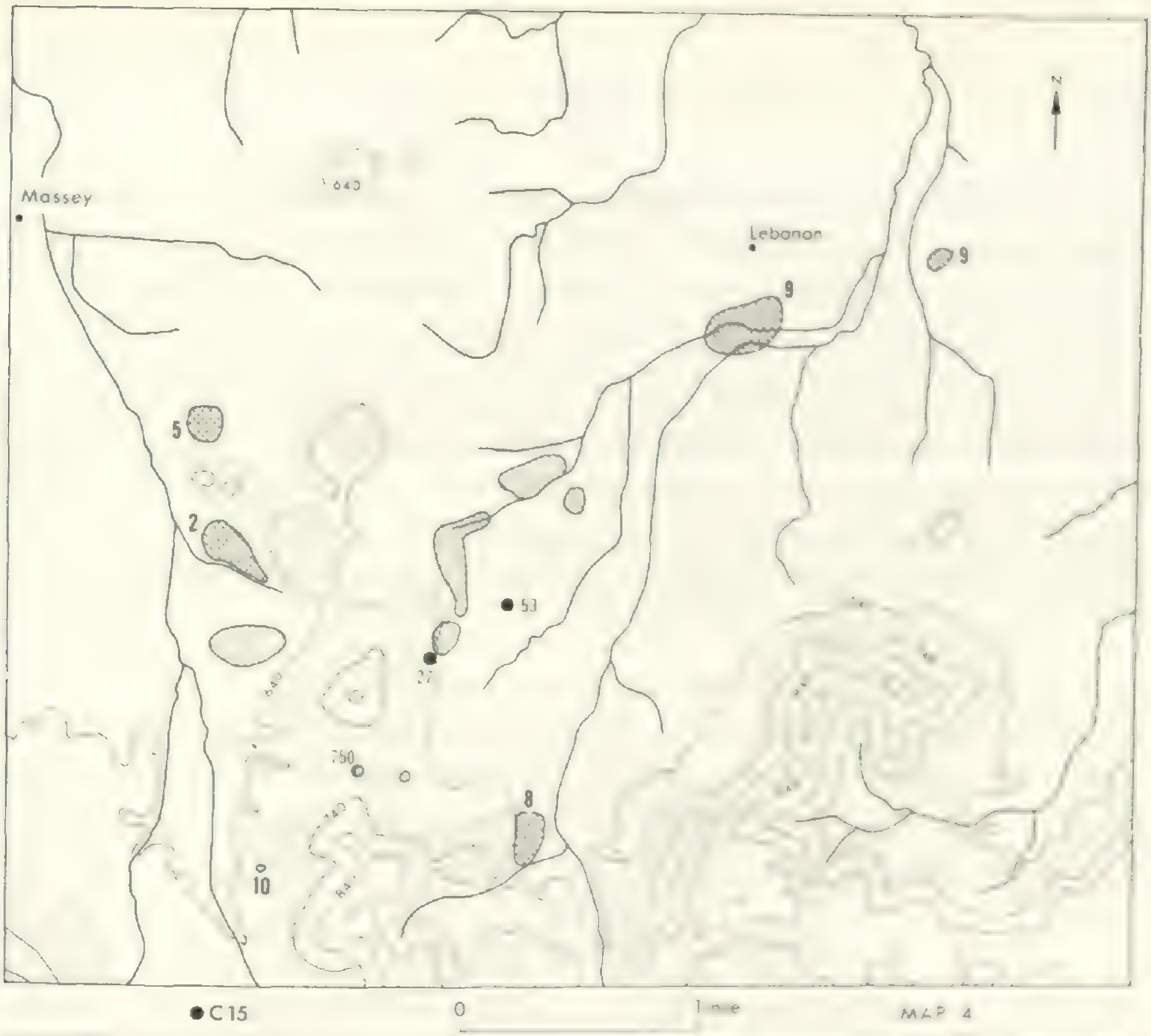
To make the following descriptions of the races of *L. crassa* and *L. alabamica* as brief as possible a character is mentioned in a description only if its expression in a particular race differs from that prevailing in most races of both species. If a character is not mentioned in a racial description, its expression is the same as that given in italics in the species description. In addition the racial averages for all measurements mentioned in the species description in italics are given for each race. Where two petal color forms (morphs) of a race were common in nature and were grown in the greenhouse in 1963, the floral measurements for each morph are given separately. More than one population of some of the races was grown, and for these races the figures given are the average of the figures for each population; in the case of silique lengths the figure given is the length of the longest fruit amongst all the field and greenhouse collections of populations of a race.

Many of the characters studied are quite variable, and the differences between races may be small. Consequently,

MAP 2

MAP 3

MAPS 2 TO 5. Distribution of the races of *L. crassa* and *L. alabamica* in the Massey-Lebanon district. The narrow lines indicate altitudes above sea level. Stippled areas indicate forest remaining around the hills. Patches of forest on the valley floor are not shown. Streams are shown in MAP 4. Cedar glades unoccupied by *L. crassa* or *L. alabamica* are indicated by crosses in MAP 2. Glade populations are



● C15 MAP 4

● A4 MAP 5

indicated by solid symbols, with the population number beside the symbol. In MAP 2 the glade populations are, from left to right, numbers 743, 89, 791, 61, 1875, 86 and 118. Populations on secondary sites are shown as hatched areas. Areas containing more than one race are cross-hatched (except the contiguous glade populations 741 and 742); the number beside each mixed population corresponds to that in the description of these areas (page 89).

some of the racial differences were not detected under the more variable conditions in nature, and appeared only in the greenhouse material, grown under relatively uniform conditions. Small differences between races have been ignored, and it is believed that all of the differences discussed represent true racial characteristics. Although many of the characters discussed appear trivial, the number of these small differences distinguishing the species and races is often surprisingly large, and provides a distinct visual impression of each race.

The description of each race is accompanied by an account of its known distribution. Pre-agricultural glade sites, and sites on cultivated land are considered separately. The hybrid swarms occurring on cultivated fields have been noted under the appropriate races.

THE RACES OF L. CRASSA

RACE C1. LAWRENCE AND MORGAN COUNTIES

Population 171 was grown in the greenhouse in 1962 and 1963.

Distinguishing features. Terminal lobes of later leaves typically crenate, varying from shallowly crenate to deeply crenate and almost lobed. Most plants of every population have yellow-centered flowers, but other flower colors are usually present in very low frequencies. Petal limbs unusually broad, approximately as wide as long. Filaments of paired stamens turn through 135-225°, anthers extrorse. Siliques narrowly oblong to oblong, with rectilinear to obtuse apices.

Branches long, 23.5 cm. Number of flowers per plant large, 465. Petals longer than in any other *L. crassa* race, 12.07 mm; emarginations deep, 0.97 mm. Styles long, 3.70 mm; pistils long, 5.83 mm. Pollen:ovule index higher than in any other race of either species, 9520. Silique longer than in any other race of *L. crassa*, up to 14.8 mm. Plants self-incompatible with some pseudo-compatibility; fraction of positive results on self-pollination 0.17, lowest of any race of either species. Percentage of flowers auto-fertilized low, 2. Advancement index 0.

Race c1 is the most primitive race of *L. crassa*, and the most similar to *L. alabamica*, especially in the length and shape of the siliques. Its distinguishing features do not indicate a particularly close relationship with any other race.

Glade sites: None is known, but the probable areas have not been thoroughly searched.

Cultivated sites: There are numerous populations in corn fields and pastures in the region one and a quarter to two and a quarter miles southwest of Speake, in Lawrence and Morgan counties. All of these populations could have come from one glade site somewhere in the vicinity of the cultivated populations, but more than one glade site may exist in the area.

RACE C2. LAWRENCE COUNTY

Population 354 was grown in 1962 and 1963.

Distinguishing features. Terminal lobes of later leaves crenate. Anthocyanin on the ventral surface of the lateral lobes of later leaves usually present, in diffuse, dense spots on the proximal lobes, concentrated on the distal lobes in a diagonal strip from the midrib to the distal margin of the lobe. Rachises of the branches grow almost horizontally from the beginning, and are stiffer and elongate more rapidly than in other races (except c4). Most plants of every population have yellow-centered flowers, but other flower colors are usually present in very low frequencies. Siliques narrowly oblong to elliptic.

Branches long, 26.5 cm. Number of flowers per plant large, 514. Petals long, 10.94 mm, emarginations deep, 0.80 mm. Styles long, 3.64 mm, pistils long, 5.95 mm. Pollen:ovule index intermediate, 4400. Siliques longer than in any other *L. crassa* race except c1, up to 13.1 mm. Plants self-incompatible with some pseudo-compatibility, fraction of positive results on self-pollination 0.21. Percentage of flowers auto-fertilized low, 2. Advancement index 5.

In a large number of measurements race c2 is not quite as primitive as race c1, but the differences are generally small, and only the difference in the pollen:ovule index is reflected in the advancement index. The geographical position of the race, the crenate terminal leaf lobes, the anthocyanin on the lateral leaf lobes, the low, stiff, rapidly elongating branches, and the relatively short styles and pistils for a self-incompatible race, suggest that race c2 is closely related to race c4. The two races are clearly separated only by the mucronate crenations of the terminal leaf lobes of race c4, and the weaker self-incompatibility of race c4.

Glade sites: An extensive glade system one and a half miles south-southwest of Danville, in Lawrence county, contains populations of race c2 which have been greatly disturbed by the removal of the surrounding forest. Other glade sites may exist to the northwest of Danville, in Lawrence county.

Cultivated sites: a large series of populations, principally in pastures, surround Danville to the west, north and east, in Lawrence and Morgan counties.

RACE C3. MORGAN COUNTY

Population 37 was grown in 1962 and 1963, and population 89 was grown in 1962.

Distinguishing features. Terminal lobes of later leaves sinuate, occasionally shallowly crenate. Primary axis of plant sometimes elongating during flowering to produce a central raceme above the rosette. Most plants of every population have yellow or yellow-centered flowers, but other flower colors are sometimes present in very low frequencies. Yellow center of yellow-centered flowers extends halfway or more along the petal limbs.

Branches long, 24.5 cm. Flowers per plant many, 404. Petals long, 11.63 mm for yellow-centered flowers, 10.47 mm for yellow flowers; emarginations deep, 0.93 mm for yellow-centered flowers, shallower, 0.50 mm for yellow flowers (but the 1962 figures show less contrast between flower colors, see table 4). Styles long, 3.85 mm for yellow-centered flowers, 4.17 mm for yellow flowers; pistils long, 6.03 mm for yellow-centered flowers, 6.35 mm for yellow flowers. Pollen: ovule index high, 6910 for yellow-centered flowers, intermediate, 5050 for yellow flowers. Siliques long, up to 12.7 mm. Plants self-incompatible with considerable pseudo-compatibility; fraction of positive results on self-pollination 0.54. Percentage of flowers auto-fertilized low, 8. Advancement index 10 (5 for plants with yellow-centered flowers, 15 for plants with yellow flowers).

Race c3 is most closely related to race c5 in its petal color polymorphism and in the long yellow portion on the petal limb of yellow-centered flowers. The latter character is also shared with race c6, but this race is quite distinct otherwise and not very similar to race c3. Only the self-incompatibility of race c3 reliably separates it from race c5. The unique elongation of the primary axis during flowering appears erratically in less than a half of the plants, but it was present in some plants every time race c3 was grown, and has been seen in nature.

Glade sites: Populations 89 and 61, one and a half miles northeast of Massey, Morgan county, are two large but considerably disturbed glades, both now continuous with derived cultivated populations. Population 743, one and a quarter miles east-northeast of Massey, is in a group of adjacent semi-isolated clearings with only a few trees between each clearing. (These clearings are considered separate populations in table 10). Population 743 probably belongs to race c3, although the frequency of pseudo-compatibility after selfing is higher than in other populations of race c3 (Lloyd, 1964).

Cultivated sites: There is a complex series of field populations to the north and east of glade populations 89 and 61. This complex of populations is continuous with the glade populations and obviously derived from them. The eastern and southern sections of this complex are separated from glade populations 86 and 118 of race c5 by a narrow line of trees and are probably a mixture of races c3 and c5 (map 2). Since the two races can only be distinguished by the presence of self-incompatibility in race c3, the extent of the contributions of race c3 and c5 to this complex is not known. Race c3 has apparently not spread south from its glade populations, since all field populations of *L. crassa* south of the race c3 glade populations are self-compatible.

RACE C4. LAWRENCE COUNTY

Population 38 was grown in 1963.

Distinguishing features. Terminal lobes of later leaves crenate; apices of the crenations mucronate. Anthocyanin on the ventral surface of the lateral lobes of later leaves usually present, in diffuse dense spots on the proximal lobes, concentrated on the distal lobes in a diagonal strip from the mid-rib to the distal margin of the lobe. Rachises of the branches growing almost horizontally from the beginning, stiffer and elongating more rapidly than in other races (except c2). Most plants of every population have yellow-centered flowers, but other flower colors may be present. Orange-centered flowers are more common than in any other race of *L. crassa*.

Branches long, 21.3 cm. Number of flowers per plant large, 407. Petals long, 11.26 mm; emarginations deep, 0.75 mm. Style length intermediate, 3.03 mm. Pistil length intermediate, 5.18 mm. Pollen: ovule index high, 5733. Silique length unknown (see below). Plants self-incompatible with considerable pseudo-compatibility; fraction of positive results on self-pollination 0.53. Percentage of flowers autofertilized low, 4. **Advancement index 15.**

Race c4 was one of the two least healthy in the 1963 greenhouse material, and the fruits were too poor for their shape and maximum length to be measured. All measurements were made on plants with yellow-centered flowers.

This primitive race is most similar to race c2, but is clearly separated from it by the mucronate crenations on the terminal lobes of the later leaves, and its weaker self-incompatibility. The relatively high frequency of orange-centered flowers (up to 25 per cent) is unique in *L. crassa.*

Glade sites: There are two known glade populations about sixty yards apart, two and a quarter miles east-northeast of Oakville, Lawrence county. There may be other glades nearby.

Cultivated sites: Race c4 has spread, probably by downstream dispersal of seeds, onto two adjacent fields one and a half miles east of Oakville.

RACE C5. MORGAN COUNTY

Populations 58 and 41 were grown in 1962 and 1963. Population 100 was grown in 1962. Populations 86 and 118 were grown in 1963.

Distinguishing features. Most plants of every population have yellow or yellow-centered flowers, but other flower colors are sometimes present in very low frequencies. Yellow center of yellow-centered flowers extends halfway or more along the petal limb.

Branches long, 24.1 cm. Number of flowers per plant large, 349. Petals long, 10.41 mm for yellow-centered flowers, shorter, 9.96 mm, for yellow flowers; emarginations deep, 1.06 mm for yellow-centered flowers, shorter, 0.89 mm, for yellow flowers. Styles long, 3.73 mm for yellow-centered flowers, slightly longer, 3.89 mm, for yellow flowers. Pistils long, 5.70 mm for yellow-centered flowers, slightly longer, 6.07 mm, for yellow flowers. Pollen:ovule index intermediate, 4340 for yellow-centered flowers, 4680 for yellow flowers. Silique length intermediate, up to 11.3 mm. Plants self-compatible, fraction of positive results on self-pollination, 0.96. Percentage of flowers auto-fertilized intermediate, 12. Advancement index 22.5 (20 for plants with yellow-centered flowers, 25 for plants with yellow flowers).

Race c5 is closely related to race c3 (see under race c3), but is somewhat more advanced in several characters. It is more distantly related to race c8.

Glade sites: Population 86, one and three-quarter miles east-northeast of Massey, is separated from the corn fields to the north only by a fence and an incomplete line of trees, and is almost continuous with the corn field populations. Population 118, one and three-quarter miles east-northeast of Massey, is about sixty yards southeast of population 86 and is also separated from the corn field populations to the north by only a narrow line of trees. Population 791, one and a half miles northeast of Massey, occupies a very marginal site about twenty yards within the forest from population 37 of race c3, and is surrounded on three sides by race c3, but it is probably a pre-agricultural site. Population 1375, one and three-quarter miles east-northeast of Massey, occurs as several scattered sub-populations in a small patch of forest in which many trees have been cut.

Cultivated sites: Race c5, like races c15 and a4, has moved long distances over cultivated fields in several directions and it has met and hybridized with several other races in these fields to produce a complicated distribution and variation pattern.

The field populations of race c5 closest to glade populations 86 and 1375 are a complex series of populations one and a half miles northeast to one and three-quarter miles east-northeast of Massey, where races c3 and c5 have come into contact as described under race c3 (see also map 2).

From population 86 and perhaps also from population 1375, race c5 has also spread south over a distance of almost two miles. There is a series of populations from a half mile east of Massey to two and one-quarter miles east-northeast of Massey. Included in this series are several populations surrounding glade population 60 of race a4, which are mixtures of race c5, race a4 and their hybrids. Also in this series are two populations, on rocky ground one and a half miles east of Massey; they may be preagricultural sites for race c5 but could equally well be secondary sites populated since the removal of forest around the outcrops.

The movement of race c5 continued south to a scattered series of populations one mile to one and three-quarter miles southeast of Massey. From the area one and three-quarter miles southeast of Massey, race c5 apparently migrated southwestwards through a narrow gap in the forest to the area one and three-quarter miles south-southeast of Massey where there are several scattered populations at present. Some of the populations of race c5 in this area are apparently unmixed with any other race of *L. crassa* or *L. alabamica*, but one contained a single race c5 × a4 hybrid plant in 1962, and the westernmost populations containing race c5 in this area are mixtures of races c5 and c15 (and possibly also c7) in varying proportions.

RACE C6. MORGAN COUNTY

Population 268 was grown in 1961 and 1962.

Distinguishing features. Base of the terminal lobe of later leaves cuneate to truncate. Plants all with yellow-centered flowers. Yellow center of flowers extending halfway or more along the petal limbs.

Branches of intermediate length, 16.5 cm. Number of flowers per plant intermediate, 241. Petals long, 10.2 mm; emarginations deep, 0.85 mm. Styles, 4.55 mm, and pistils, 6.90 mm, longer than in any other race of either species. Pollen:ovule index low, 3620. Silique length intermediate, up to 11.0 mm. Plants self-compatible, fraction of positive results on self-pollination, 0.99. Percentage of flowers auto-fertilized intermediate, 0.16. Advancement index 30.

Race c6 is geographically the most isolated of all *L. crassa* races, and it is not particularly closely related to any other race. The leaves are quite distinct, even though I could find only one constant tangible difference between them and those of other races. The long yellow center of the flowers may indicate a relationship to races c3 and c5.

Glade sites: None is known. One or more must exist, almost certainly to the west of the cultivated site, but all attempts to find a glade site failed.

Cultivated sites: This race is known only from two adjacent fields constituting population 268, three miles southwest of Massey, Morgan Co.

RACE C7. MORGAN COUNTY

Population 361 was grown in 1963.

Distinguishing features. Terminal lobes of later leaves shallowly crenate to crenate. Terminal lobes, and especially the lateral lobes of later leaves, slightly incurved exposing the paler edges of the leaves. Most plants have yellow-centered or yellow flowers but other color forms are present. Stigma and anthers of paired stamens at approximately the level of the petal limbs. Filaments of paired anthers turn through 135° or sometimes less, anthers extrorse or slightly introrse.

Branches of intermediate length, 18.9 cm. Number of flowers per plant large, 361. Petals long, 10.33 mm; emarginations deep, 0.90 mm. Styles, 2.21 mm, and pistils, 4.23 mm, shorter than in any other race of *L. crassa*. Pollen:ovule index intermediate, 4120. Siliques short, up to 9.3 mm. Plants self-compatible, fraction of positive results on self-pollination 0.95. Percentage of flowers auto-fertilized intermediate, 15. Advancement index 40.

All measurements were made on plants with yellow-centered flowers.

Race c7 is not particularly similar to any other, but the incurved leaf lobes may indicate a closer relationship to the adjacent race c14 than to any other.

Glade sites: Population 361, one mile southeast of Massey, is probably a pre-agricultural site, although the forest around it has been completely destroyed, and the population has probably expanded beyond its pre-agricultural size.

Cultivated sites: The area immediately to the south and west of population 361 contains a complex group of populations with contributions from races c7 and c15 (and probably also race c5). The area one and a half to one and three-quarter miles southeast of Massey contains at least one population (298) of race c7 which must have come around the forest between populations 298 and 361. The margin of population 298 is only about six yards from a small scattered population (276) of race a4, and in 1961 there were a number of obviously hybrid plants near the margins of the two populations. Other nearby populations may contain elements of race c7 (see under race c5).

RACE C8. MORGAN COUNTY

Population 72 was grown in 1962 and 1963.

Distinguishing features. Terminal lobes of later leaves cordate, crenate. Most plants have yellow or yellow-centered flowers, but other flower colors are present in very low frequencies. Anthers of paired stamens often widely separated from each other and the stigma.

Branches of intermediate length, 14.0 cm. Number of flowers per plant intermediate, 225. Petals of yellow-centered flowers long, 10.78 mm, those of yellow flowers considerably shorter, 8.73 mm; emarginations of yellow-centered flowers of intermediate depth, 0.69 mm, those of yellow flowers much shallower, 0.42 mm. Styles of intermediate length, 3.21 mm for yellow-centered flowers, slightly longer, 3.57 mm, for yellow flowers; pistils of intermediate length, 5.39 mm for yellow-centered flowers, slightly longer, 5.52 mm, for yellow flowers. Pollen:ovule index intermediate, 4510 for yellow-centered flowers, low, 3360 for yellow flowers. Siliques short, up to 8.8 mm. Plants self-compatible; fraction of positive results on self-pollination 0.98. Percentage of flowers auto-fertilized intermediate, 10. Advancement index 47.5 (40 for plants with yellow-centered flowers, 55 for plants with yellow flowers).

Race c8 is probably most closely related to races c3 and c5, but is considerably more advanced in many features than either of them. It is outstanding in the marked difference between yellow-centered and yellow flowers in petal length, petal emargination depth, and style length.

Glade site: None is known, though the land surrounding the only known cultivated population was carefully searched.

Cultivated site: This race is known only from population 72, on grazed land half a mile west of Lebanon, Morgan county.

RACE C9. MORGAN COUNTY

Population 769 was grown in 1963.

Distinguishing features. Terminal lobes of later leaves always cordate, often wider than long, entire or slightly sinuate. Lateral lobes of later leaves, especially the distal ones, usually with an irregular line of anthocyanin at right angles to the mid-rib (line often broken, less prominent than in race c11). All plants have yellow-centered flowers. Filaments of paired stamens turn through at least 180°, usually through 225°, so the two anthers of a stamen pair are together and face in the same direction, at right angles to anthers of the single stamens (fig. 6). Apices of the siliques sometimes rounded, more often truncate.

Branches of intermediate length, 15.5 cm. Number of flowers per plant intermediate, 217. Petals moderately long, 9.77 mm; emarginations deep, 1.06 mm. Styles short, 2.53 mm; pistils short, 4.66 mm. Pollen:ovule index low, 3560. Siliques short, up to 0.97 mm. Plants self-compatible, fraction of positive results on self-pollination 0.94. Percentage of flowers auto-fertilized intermediate, 10. Advancement index 50.

Race c9 is most closely related to race c11 (see under race c11) but is more primitive.

Glade site: Population 769, one and a half miles east-southeast of Massey, Morgan county, is the only glade site.

Cultivated site: Population 771 is a small population about fifty yards downhill from population 769, just outside the forest margin.

RACE C10. MORGAN COUNTY

Population 698 was grown in 1963.

Distinguishing features. Mature later leaves strongly curved, always in a counter-clockwise direction when looking down on the plant and considering the leaf from the petiole towards the terminal lobe. These leaves also rotated, so the terminal lobe is at an angle of about 45° or more to the horizontal plane, with the ventral surface facing outwards from the curvature. Terminal lobes of later leaves entire, polygonal (heptagonal to octagonal); angles apiculate. Plants with yellow or yellow-centered flowers. Petal limbs usually bend at less than 90° to the claws in open flowers. Yellow center of yellow-centered flowers not as bright as in other races (cf. race c14). Orange pigment of nectar guides poorly developed, sometimes completely masked by the brown pigment. Lateral nectar guides much shorter than the central one. Filaments of paired stamens turn through 135°, sometimes less, anthers extrorse or slightly introrse.

Branches of intermediate length, 11.0 cm. Number of flowers per plant small, 126. Petals long, 10.02 mm; emarginations of intermediate depth, 0.61 mm. Style length intermediate, 3.29 mm; pistil length intermediate, 5.10 mm. Pollen:ovule index low, 3690. Siliques short, up to 9.4 mm. Plants self-compatible, fraction of positive results on self-pollination 0.95. Percentage of flowers auto-fertilized high, 30. Advancement index 70.

No yellow-flowered plants were sufficiently healthy in the 1962 material for measurements to be taken from them. The flower measurements above refer only to yellow-centered flowers. Race c10 closely resembles the geographically adjacent race c14 in its floral characters but differs in having a petal color polymorphism and in its very distinctive leaf shape and curvature.

Glade site: Population 698, one and a half miles southeast of Massey, is the only known population.

Cultivated site: None is known, and it seems unlikely that any have ever been produced since population 698 is surrounded by forest.

RACE C11. MORGAN COUNTY

Population 742 was grown in 1963.

Distinguishing features. Mature leaves short, usually less than 7 cm long. Terminal lobes of later leaves wider than long, cordate, entire or slightly sinuate, closely appressed to the ground. Lateral lobes of later leaves, especially the distal ones, usually with a conspicuous line of anthocyanin at right angles to the mid-rib. Branches extremely short, not exceeding the scapes of the central flowers, but the flowers are not densely crowded as in race c13. All plants with yellow-centered flowers (but see distribution below). Petal limbs usually bend at less than 90° to the claws in open flowers. Stigma and anthers of paired stamens at approximately the level of the petal limbs.

Branches shortest of any race of either species, 4.1 cm. Number of flowers per plant small, 163. Petals of intermediate length, 9.56 mm; emarginations of intermediate depth, 0.71 mm. Styles short, 2.68 mm; pistils short, 4.45 mm. Pollen:ovule index low. 3910. Siliques short, up to 8.8 mm. Plants self-compatible, fraction of positive results on self-pollination 1.00. Percentage of flowers auto-fertilized high, 21. Advancement index 75.

Race c11 is very distinct, but the cordate and entire or sinuate terminal leaf lobes and prominent anthocyanin on the lateral leaf lobes shared with the geographically adjacent race c8 indicate that these two races are more closely related to each other than to any other race.

Glade site: Population 742, one and a half-miles east-southeast of Massey, and about 80 yards southeast of population 769 (race c8), is the only known glade population; it is in the process of fusing with population 741 (race c12?) — see page 94.

Cultivated site: None is known, and the position of population 742 within the forest makes it unlikely that any have ever been produced.

RACE C12. MORGAN COUNTY

Population 739 was grown in 1963.

Distinguishing features. All plants have yellow flowers. Petal limbs oblong to obovate, often bending at more than 90° to the claw in open flowers, and rotated so that the limbs of the anterior petals are inclined towards each other and the limbs of the posterior petals are inclined towards each other. In flower closing, petal limbs often bend back past the vertical plane until they become horizontal over the pistil, and are stacked like the four sections of the top of a cardboard box. All siliques (greenhouse grown material only) with one (or occasionally more) holes in the septum.

Branches short, 7.1 cm. Number of flowers per plant small, 144. Petals shortest of any race of either species, 7.8 mm; emarginations shallow, 0.44 mm. Styles short, 2.61 mm; pistils short, 4.55 mm. Number of pollen grains per ovule few, 3920. Siliques short, up to 9.2 mm. Plants self-compatible; fraction of positive results on self-pollination 1.00. Percentage of flowers auto-fertilized high, 24. Advancement index 80.

The yellow flowers and rather short and narrow leaves of race c12 indicate that it is probably most closely related to the geographically adjacent race c13, but it is unique and very distinctive in its short petals, peculiar and complicated petal movements, and the invariably present silique septum hole (the latter is not invariably present in siliques collected in nature).

Glade sites: Population 739, one and a half miles southeast of Massey, consists of two separate subpopulations in the same glade about thirty yards apart. Population 741, one and a half miles east-southeast of Massey is now merging with population 742 of race c11 (see page 94). The fruits of population 741 collected in nature resemble those of race c12 rather than those of race c13, but the identity of populations 739 and 741 needs checking.

Cultivated site: None is known, and as both populations are more than forty yards within the forest margin it is unlikely that any have ever been produced.

RACE C13. MORGAN COUNTY

Population 745 was grown in 1963.

Distinguishing features. Mature later leaves short, usually less than 7 cm long. Terminal lobes of later leaves cuneate to obtuse, margin unusually variable, sinuate to deeply crenate or even lobed. Branches short, not extending beyond the scapes of the central flowers, almost vertical, scapose and racemose flowers densely crowded together. All plants yellow-flowered. Sepals often open to a horizontal position before the petals unfold. Petal limbs usually bend at less than 90° to the claws in open flowers. Filaments of paired stamens turn through 90° (occasionally more or less), anthers introrse. Siliques oblong to elliptic or ovate, apex acute to obtuse.

Branches short, 8.8 cm. Number of flowers per plant small, 196. Petal length intermediate, 9.52 mm, emarginations deep, 0.82 mm. Style length intermediate, 3.19 mm; pistil length intermediate, 5.29 mm. Pollen:ovule index low, 3240. Siliques short, up to 9.2 mm. Plants self-compatible; fraction of positive results on self-pollination 1.01. Percentage of flowers auto-fertilized high, 20. Advancement index 80.

Race c13 is probably most closely related to the geographically adjacent race c12, but it is very distinctive in the (sometimes) deeply incised terminal lobes of the leaves, the crowded inflorescences, and the (sometimes) delayed opening of the petals.

Glade sites: Population 745, one and a half miles southeast of Massey, is about fifty yards south of population 739 (race c12) and separated from it by continuous forest. Population 746 is west of population 745, and the edges of the two populations are separated by about twenty yards of forest. These two populations are sufficiently isolated to be distinct, but population 746 was not grown in the greenhouse, so it is provisionally included in this race.

Cultivated site: None is known, and as both populations 745 and 746 are well within the forest margin it is unlikely that any have ever been produced.

RACE C14. MORGAN COUNTY

Population 699 was grown in 1963.

Distinguishing features. Terminal lobes and especially the lateral lobes of later leaves slightly incurved exposing the paler edges of the leaves. Mature later leaves sometimes slightly curved (cf. race c10). All plants with yellow-centered flowers. Petal limbs usually bend at less than 90° to the claws in open flowers. Yellow center of flowers not as bright as in other races (cf. race c10). Orange pigment of nectar guides poorly developed, sometimes completely masked by the brown pigment. Lateral nectar guides much shorter than the central one. Filaments of paired stamens turn through 90 to 135° so the anthers are introrse to extrorse.

Branches rather short, 10.2 cm. Number of flowers per plant small, 115. Petals short, 8.13 mm, emarginations shallow, 0.47 mm. Style length intermediate, 3.20 mm; pistil length intermediate, 5.0 mm. Pollen:ovule index low, 3480. Silique length unknown (see below). Plants self-compatible; fraction of positive results on self-pollination 1.00. Percentage of flowers auto-fertilized high, 22. Advancement index 85.

This population was one of the two least healthy in the 1963 greenhouse material, and the fruits were considered too poorly developed to describe and measure.

Race c14 closely resembles race c10 in its floral characters, but it is monomorphic and the distinctive leaf curvature of race c10 is barely evident in race c14, and the shape of the terminal lobes of the later leaves is very different in races c10 and c14. Race c14 appears to be more advanced than race c10 in a number of characters.

Glade site: Population 699, one and a half miles southeast of Massey, is the only known glade site. It is only about twenty-five yards north of population 698 (race c10) and separated from it by an incomplete line of trees. Even so these two populations have remained distinct and must be effectively geographically isolated.

Cultivated site: Population 700 is about 100 yards north of population 699 in a field which had not been ploughed for some years prior to 1962. It consisted in 1962 of a few scattered plants with introrse anthers, apparently of race c14. An unused forest road exists between population 699 and this field and the plants could easily have moved along it.

RACE C15. MORGAN COUNTY

(*L. crassa* var. *elongata* Rollins)

Population 370 was grown in 1962 and 1963. Populations 53 and 750 were grown in 1963.

Distinguishing features. Terminal lobes of later leaves sinuate, occasionally shallowly crenate. All plants yellow-flowered. Petal limbs almost always bend at less than 90° to the claws in open flowers. Filaments of paired stamens turn through 90° (occasionally more or less), anthers introrse. Siliques oblong to elliptic, apices rectilinear to round.

Branches short, 7.1 cm. Number of flowers per plant smallest of any race of either species, 110. Petals short, 8.69 mm, emarginations shallower than in any other race of either species, 0.35 mm. Styles short, 2.50 mm; pistils short, 4.65 mm. Pollen:ovule index lowest of any *L. crassa* race, 3010. Silique length intermediate, up to 11.6 mm. Plants self-compatible; fraction of positive results on self-pollination, 0.97. Percentage of flowers auto-fertilized high, 27. Advancement index 100.

Race c15 is the most consistently advanced of any race of either species, but even this race is only moderately advanced in silique length. It does not appear to be particularly closely related to any other race.

Glade sites: Population 53 is one and three-quarter miles south-southwest of Lebanon. Population 27, two and a half miles southwest of Lebanon, occupies a greatly disturbed limestone outcrop which is probably a pre-agricultural site. Population 750, two and three-quarter miles southwest of Lebanon, occupies a high (700 ± 5 feet above sea level) site on the brink of a quarry, and on a forest road; this site is doubtfully pre-agricultural.

Cultivated sites: In 1961 there were two separate populations of race c15 in the area two and a half miles south-southwest of Lebanon (map 4). One of these was a mixture of plants of races c15 and a4 and their hybrids. The other was a small but vigorously growing population in a grazed field; but in 1962 and 1964 there were no plants there at all. A series of populations extends from population 27 to the northeast for a distance of almost three miles. This distribution pattern is admirably explained by the movement of race c15 seeds downstream from population 27 (Rollins, 1963). The populations farthest from population 27 are a mixture of races c15 and a4 (map 4).

There are several populations of race c15 in the area one mile southeast of Massey. These are mixtures of race c15 and race c7.

There are several populations containing race c15 in the area one and a half to two miles south-southeast of Massey. In addition to the populations with elements from races c5 and c15 (and c7?—map 4) there are a number of populations of race c15 alone.

The southernmost population containing race c15, population 275, two and three-quarter miles south-southeast of Massey, in 1961 had a few yellow-flowered plants which were hybrids between race c15 and race a3 and/or race a4 (see under race a3). These plants in population 275 are apparently a relict of populations which must have spread overland from the race c15 populations to the north.

THE RACES OF L. ALABAMICA

RACE A1. FRANKLIN AND LAWRENCE COUNTIES

Population 81 was grown in 1962. Populations 81, 82 and 923 were grown in 1963.

Distinguishing features. All plants with yellow-centered flowers in most populations; several populations also have other flower colors in low frequencies. Anthocyanin always present on the dorsal surface of petal limbs of yellow-centered flowers.

Branches long, 29.3 cm. Number of flowers per plant large, 503. Petals longest of any race of either species, 12.62 mm; emarginations deep, 1.09 mm. Styles short, 2.44 mm; pistils long, 5.61 mm. Pollen: ovule index high, 7030. Siliques very long, up to 30.0 mm. Plants self-incompatible with some pseudo-compatibility; fraction of positive results on self-pollination, 0.22. Percentage of flowers auto-fertilized low, 2. Advancement index 0.

All measurements were made on plants with yellow-centered flowers.

Race a1 is the most primitive race of *L. alabamica*, and apart from the pistil and fruit differences between the two species there is only a minor difference in the leaf margins separating this race and race c1. Races a1 and a2 are very similar, although race a2 is slightly more advanced in having lower measurements for several characters; but the only character which reliably separates them is the self-compatibility of race a2.

Glade sites: There are four separate areas where several or many glade populations exist. These glade populations, like those of race a2, occur on extensive areas of flat outcrops and are frequently more or less continuous for a hundred yards or more. These populations resemble those of *L. stylosa* in Tennessee in their size and extent more than they do the small discrete populations of *L. crassa* and *L. alabamica* elsewhere.

One series of glades is around Mehama on the Franklin-Lawrence county border. A second series of glade populations (including population 923) is approximately two miles west of Mt. Hope, around the Franklin-Lawrence county border. The most extensive series of glade populations (including populations 81 and 82) occurs in a belt almost two miles wide (north to south) from Waco to Newburg in Franklin county. A fourth series of glades occurs in the vicinity of Isbell, Franklin county; these are smaller than the previous glades and occur on the lower slopes of hills.

Cultivated sites: There are field populations nearby, and apparently derived from each of the glade areas of race a1. In addition a population one mile northeast of Tharptown, Franklin County, and several populations two to six miles east of Isbell are some distance from any of the known glades and may be derived from unknown glade populations.

RACE A2. FRANKLIN COUNTY

Population 918 was grown in 1963.

Distinguishing features. All plants with yellow-centered flowers in most populations; one population, *Rollins and Channell 5642*, had two yellow-flowered plants in 1956. Anthocyanin always present on the dorsal surface of petal limbs.

Branches long, 21.6 cm. Number of flowers per plant intermediate, 297. Petals long, 12.06 mm, emarginations deep, 0.88 mm. Styles short, 2.56 mm; pistils long, 6.62 mm. Pollen:ovule index intermediate, 4180. Siliques very long, up to 37.9 mm. Plants self-compatible, fraction of positive results on self-pollination 0.87. Percentage of flowers auto-fertilized intermediate, 19. Advancement index 25.

Race a2 is most closely related to race a1 but is distinct from the latter in being self-compatible, and slightly more advanced in several other characters.

Glade sites: The glade populations of race a2, like those of race a1, are extensive and more or less broken up into sub-populations scattered on bare outcrops that may be up to a hundred yards long. Two separate areas of glade populations are known, though there may be more. One of these is in the area one to three miles south-southeast of Landersville; the other is approximately three miles south of Hatton.

Cultivated sites: The glades near Landersville have given rise to a number of populations in the vicinity of Landersville, and possibly also to scattered field populations between Monk City and Moulton. Other populations three miles southwest of Moulton and three miles south of Moulton may be derived from the glade populations near Landersville or from other unknown glade populations farther east. The glades south of Hatton have also given rise to a number of populations in nearby fields.

RACE A3. MORGAN COUNTY

Population 275 was grown in 1963.

Distinguishing features. Mature leaves short, usually less than 8 cm. Terminal lobes of later leaves obtuse to cuneate. Lateral lobes of later leaves, especially the distal ones, have a prominent diagonal strip of dense, sometimes confluent, spots of anthocyanin running from the midrib to the distal margin of each lobe. All plants have yellow-centered flowers. Anthocyanin always present on the dorsal surface of the petal limbs. Petal limbs usually wide, approximately as wide as long. Siliques oblong.

Branches of intermediate length, 18.5 cm. Number of flowers per plant intermediate, 295. Petals long, 11.19 mm, emarginations deep, 1.02 mm. Styles short, 2.65 mm; pistils long, 5.75 mm. Pollen:ovule index intermediate, 4130. Siliques long, up to 23.4 mm. Plant self-compatible; fraction of positive results on self-pollination, 0.99. Percentage of flowers auto-fertilized intermediate, 14. Advancement index 30.

Race a3 is not closely related to any other race. The leaves of the plants are very distinctive. The seeds were collected from the eastern section of population 275 (see below).

Glade site: None is known, although the forest margin adjacent to the cultivated site was carefully searched.

Cultivated site: Population 275, two and three-quarter miles south-southeast of Massey, is the only known site of this race. The glade source may be some distance to the north since both races c15 and a4 have also reached this area from that direction.

Population 275 has received a small element of plants from race c15, and a larger element more recently from race a4. But in both 1961 and 1962 the eastern section of this population, about twenty yards by thirty yards long, contained only plants with intense anthocyanin coloration on the dorsal surface of the petal limbs, and with extrorse anthers, *i.e.*, they apparently consisted entirely of plants of race a3.

RACE A4. MORGAN COUNTY

(*L. alabamica* var. *brachystyla* Rollins)

Population 445 was grown in 1963.

Distinguishing features. Terminal lobes of later leaves often longer than broad, deeply and broadly sinuate or almost trilobed with an obtuse to rounded apex. All plants with yellow-centered flowers. Petals limbs have no anthocyanin. Petal limbs of open flowers usually incurved, almost always bending at less than 90° to the claws in open flowers. Filaments of paired stamens turn through 90° (occasionally more or less), anthers introrse. Siliques oblong.

Branches long, 23.8 cm. Number of flowers per plant intermediate, 295. Petal length intermediate, 9.26 mm, emarginations shallow, 0.33 mm. Styles shortest of any race of either species, 1.98 mm; pistil length intermediate, 5.26 mm. Pollen:ovule index lowest of any race of either species, 2770. Siliques long, but shortest of any race of *L. alabamica,* up to 17.6 mm. Plants self-compatible; fraction of positive results on self-pollination, 0.97. Percentage of flowers autofertilized intermediate, 18. Advancement index 70.

Race a4 occurs the farthest east of all *L. alabamica* races and is the most advanced of the *L. alabamica* races grown in the greenhouse. It is quite distinctive in its leaf shape particularly, and does not appear to be closely related to any other race.

Glade sites: Race a4 is known from more glade sites than any other race in the Massey-Lebanon district (see map 5) and these sites are widely scattered in the area. The following are probably all of pre-agricultural age, though all of them are considerably disturbed now.

Population 288 is two and three-quarter miles south-southeast of Massey. Population 60 is one and a half miles east of Massey and now contains race c5 also, which has reached the area following the removal of forest. Population 681 is three-quarters of a mile west-northwest of Lebanon. Population 445 is one and three-quarter miles south-southeast of Lebanon. Population 684 is two miles south-southeast of Lebanon. Population 685 is one and a half miles southeast of Lebanon.

Cultivated sites: Several of the glade sites have produced more or less extensive series of derived populations on cultivated land, and several hybrid combinations with other races have resulted.

Glade population 288 has given rise to a more or less continuous chain of plants extending around the forest margin to the west and south to population 275, two and three-quarter miles south-southeast of Massey, where race a4 has mixed with races c15 and a3. A population of race a4 (with race a4 × c7 hybrids — see under race c7) one and a half miles south-southeast of Massey is also probably derived from glade population 288 by overland dispersal with subsequent elimination of the intervening populations.

Glade population 60, on an outcrop from which the surrounding forest has been completely removed, has spread in all directions for short distances and formed many field populations mixed with race c5 plants.

The remaining field populations of race a4 are probably derived from one or more of the glade populations 445, 684 and 685. A population two and a half miles south-southwest of Lebanon contains race c15, race a4 and hybrid plants. Other populations two and a quarter miles south of Lebanon and one and a quarter miles southeast of Lebanon contain only race a4 plants. The series of populations of race a4 from a quarter of a mile southwest of Lebanon to one mile east of Lebanon may have come either overland or downstream from one of the glades to the south; some of these populations contain varying numbers of race c15 plants and c15 × a4 hybrids.

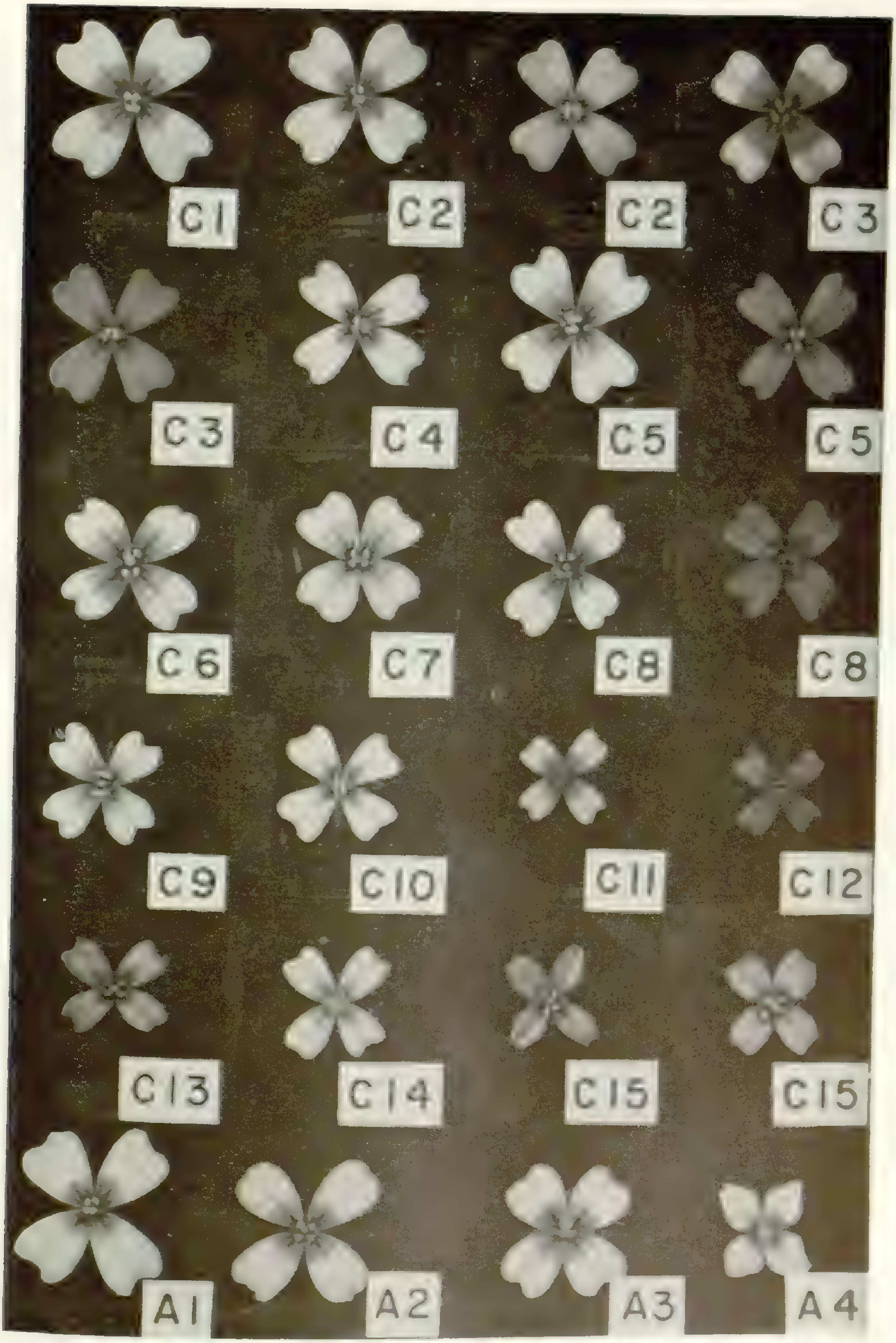


FIG. 3. Flowers of all the described races of *L. crassa* and *L. alabamica*. Both yellow and yellow-centered flowers of races c2, c3, c5 and c8 are shown. Flowers of two populations (370 and 750) of race c15 are shown. ca. × [illegible].

FIG. 4. Flowers of all the described races of *L. crassa* and *L. alabamica* viewed from the side (facing paired anthers). Two petals and a sepal have been removed from each flower. A flower of race c13, with open sepals and closed petals, is also shown. *ca.* × ¾.

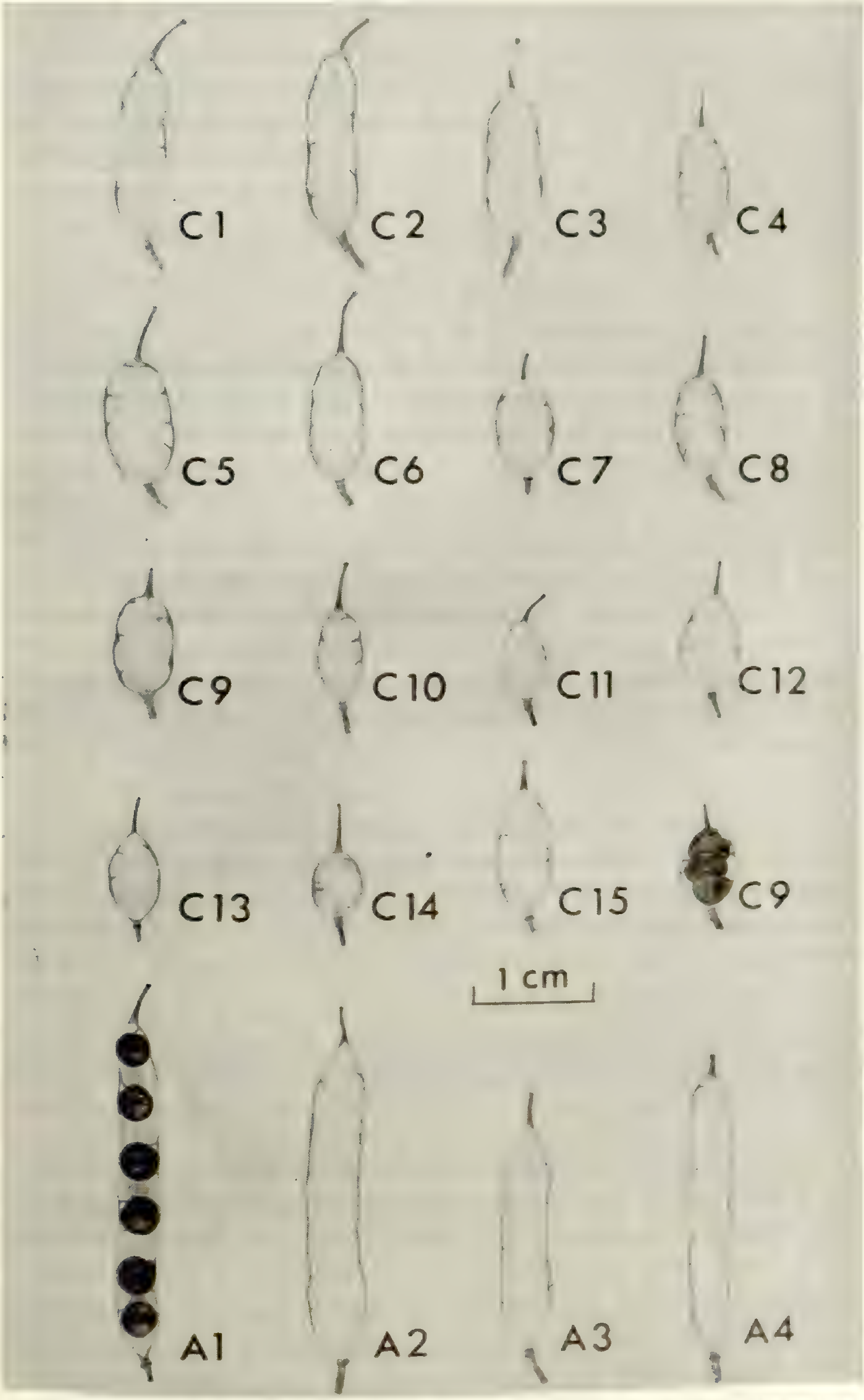


FIG. 5. Dehisced fruits of all the described races of *L. crassa* and *L. alabamica*. The seeds in one locule are shown for race c9 of *L. crassa* and race a1 of *L. alabamica*.

UNDESCRIBED RACES OF L. ALABAMICA

Two additional races of *L. alabamica* have been distinguished in the field but not grown in the greenhouse. They therefore can not be described fully, or be given an advancement index. Both races have been designated by the town nearest which they occur, and their distinguishing features and known distributions are briefly indicated.

A. THE 'RUSSELLVILLE RACE' OF L. ALABAMICA

In 1964 a population of *L. alabamica* which was clearly different from all other known populations was discovered in a ploughed field three and a half miles northeast of Russellville, Franklin County. This field is in a narrow valley with steep hills on either side. The glade source is unknown but is probably at or near the base of the hills, and is clearly separated from the glades of race a1 to the east and south by several miles of hilly ground unsuitable for *Leavenworthia*. The Russellville race appears to be approximately as advanced in characters associated with the breeding system as is race a4, but is easily distinguished from race a4 by the presence of anthocyanin on the petal limbs. The terminal lobes of later leaves appear to be relatively broader than those of race a4. The flowers are approximately the same size as those of race a4, and are mostly yellow-centered; but plants with orange-centered flowers (unknown in other *L. alabamica* races) are quite common. The petal limbs usually bend at less than 90° to the claws in open flowers, and are often incurved (*cf.* race a4). The filaments of paired stamens turn through 90° so the anthers are introrse. The styles are approximately as long as those of race a4. Forty-four self-pollinated flowers all gave positive results, so the plants are self-compatible.

B. THE 'TUSCUMBIA RACE' OF L. ALABAMICA

A number of populations southwest and west of Tuscumbia, Colbert County, are probably distinct from other races of *L. alabamica*, but have not been grown in the greenhouse. These occur in or near scattered glades from 13 miles west of Tuscumbia to four miles southwest of Tuscumbia (Rollins, 1963). It is possible that the separate populations are not all identical, but I have examined only the population four miles southwest of Tuscumbia. This population appears to be somewhat more advanced than either race a4 or the Russellville race in characters associated with the breeding system. It can be distinguished from race a4 by the presence of anthocyanin on lower surface of the petal limbs, and from the Russellville race by the much shorter and less conspicuous nectar guides and yellow portions of the petal limbs. All of the flowers examined were yellow-centered, and approximately as large as those of race a4. The petal limbs of open flowers are often incurved, and bend at less than 90° to the petal claws. The filaments of paired stamens turn through 90° so the anthers are introrse. The styles are approximately as long as those of race a4 and the Russellville race. Thirty-four of thirty-five self-pollinated flowers gave positive results, so the plants are self-compatible.

Race a4 and the Russellville and Tuscumbia races of *L. alabamica* share several common features which distinguish them from the more primitive races (a1, a2 and a3) of *L. alabamica,* viz. short petals and styles, incurved, incompletely opening petal limbs, and introrse anthers (paired stamens). It is possible that these three races form a natural group within *L. alabamica,* but these common features could equally well result from parallel evolution towards features associated with increasing autogamy. The presence of race a3 near race a4, and of race a1 near the Russellville race, perhaps suggests that race a4, the Russellville and Tuscumbia races have become advanced in characters associated with self-compatibility independently of each other, but the relationships between the three races can not be settled until all have been studied in the greenhouse.

THE EVOLUTION OF SELF-COMPATIBILITY IN L. CRASSA AND L. ALABAMICA

Rollins (1963) discovered the presence of self-incompatible and self-compatible races in both *L. crassa* and *L. alabamica.* The direction of evolution in these species has almost certainly been from self-incompatibility to self-compatibility, since race c1 of *L. crassa* possesses a sporophytic, one locus, multiallelic incompatibility system (Lloyd, unpublished). This type of incompatibility system is uncommon, and is known only in the *Cruciferae* and *Compositae,* so it is unlikely to have been acquired independently in *Leavenworthia.*

In the present study controlled cross- and self-pollinations were made in the field and greenhouse on all the races of *L. crassa* and *L. alabamica* described above. In three series of tests — in the field in 1962 and in the greenhouse in 1962 and 1963 — the resulting pollen tube growth in each style was examined. In two other series of tests, in the greenhouse in 1962 and 1963, the subsequent silique growth and seed set was examined.

For the pollen tube growth tests the pedicel of one flower bud from each of a number of plants of a population was cut off the afternoon before the flower was due to open and put into a vial containing water. The next morning, when the anthers had dehisced, pollen was transferred to the stigmas with an arrowhead needle until they were abundantly covered with pollen. About 2/3 of the flowers of each sample were self-pollinated, and the remainder were cross-pollinated. The needle was cleaned after each pollination, and the flowers put back in the vials. In the greenhouse tests additional flowers from the same plants were pollinated each day until about 40 self-pollinations had been made on each population.

The styles were cut off approximately 24 hours after pollination and put into a solution of lactophenol containing traces of acid fuchsin and fast green. After another 24 hours or longer the styles were examined under a microscope to see if there were any pollen tubes in the style. The self-incompatibility barrier in *Leavenworthia,* as in other *Cruciferae,* is at the stigma. If there were any tubes at all present in the style, the pollination was considered as successful and counted as a positive result. With few exceptions the styles contained either no pollen tubes or a considerable number, usually more than thirty.

The fraction of positive tests from self-pollinations of the flowers of a population was calculated. If more than one population of a race was tested in one series, the geometric mean of the fraction of positive results on self-pollination in each population was calculated. The cross-pollinations showed that there were almost no failures due to poor pollen or unsuitable pollinating conditions. In the 1962 field tests 333 out of 336 (99 per cent) of the cross-pollinations on all populations gave positive results. In the 1962 greenhouse tests 403 of 407 (99 percent) cross-

TABLE 1. TESTS ON THE FRACTION OF POSITIVE RESULTS ON SELF-POLLINATION

Species and Race	1962 Field Tests	1962 Greenhouse Tests		1963 Greenhouse Tests		Geometric Mean of all Tests	Selfing Status[1]
	By pollen-tube growth	By pollen-tube growth	By silique growth	By pollen-tube growth	By silique growth		
L. crassa							
c1	0.33**	0.05**	0.19**	0.27	0.16**	0.17	-
c2	0.06**	0.47	0.27**	0.21	0.28**	0.21	-
c3	0.69	0.59**	0.34**	0.35	0.92	0.54	-
c4	0.83	—	—	0.30	0.59**	0.53	-
c5	0.97	0.98	0.95	0.94	0.96	0.96	+
c6	1.00	0.95	1.01	1.00	1.00	0.99	+
c7	1.00	—	—	0.86	1.00	0.95	+
c8	0.91	1.00	1.01	0.99	1.00	0.98	+
c9	1.00	—	—	0.83	1.00	0.94	+
c10	1.00	—	—	0.91	0.93	0.95	+
c11	1.00	—	—	1.00	1.00	1.00	+
c12	1.00	—	—	0.96	1.07	1.00	+
c13	1.00	—	—	1.00	1.05	1.01	+
c14	1.00	—	—	1.00	—	1.00	+
c15	0.99	0.96	1.00	0.93	0.91	0.97	+
L. alabamica							
a1	0.12**	0.34**	0.19**	0.06	0.29**	0.18	-
a2	1.00	—	—	0.93	0.71	0.87	+
a3	0.97	—	—	1.00	1.00	0.99	+
a4	1.00	—	—	0.91	1.00	0.97	+

[1] - = self-incompatible (with various frequencies of psuedo-compatibility)
+ = self-compatible

** The fraction of positive results was significantly lower ($P<.01$) on self-pollination than on cross-pollination.

pollinations on all populations gave positive results. These figures are so close to 100 per cent that it was considered unnecessary to do any cross-pollinations in the 1963 greenhouse tests by pollen tube growth.

In the greenhouse tests on the growth of siliques after cross- and self-pollination, the flowers to be pollinated were emasculated the evening of the day before they would open. The next day the stigmas were examined with a hand lens to check that there were no pollen grains on them, and pollen from another flower of the same plant or of a different plant of the same population was put on each stigma with an arrowhead needle. The flowers were not bagged, either before or after pollination, since the greenhouse was insect-free.

When the pollinated flowers were examined about 5 weeks later there was a clear distinction between those that had been fertilized and contained one or more seeds in an enlarged silique, and those that had not been fertilized, in which neither the ovary nor the ovules had enlarged. For each plant, the fraction of positive results on self-pollination (*i.e.,* the fraction of flowers fertilized) divided by the fraction of positive results on cross-pollination, was calculated. This figure, which may be called the relative fraction of positive results on self-pollination, corrects the self-pollination results for occasional failures due to poor pollinating conditions. As an extra precaution against the possibility of incompatible cross-pollinations, the few plants on which less than 3/4 of the cross-pollinations succeeded were eliminated from the results.

In most populations, controlled pollinations were done on between four and ten plants in either 1962 or 1963. The geometric means of the relative fractions of positive results on self-pollination, for all the plants of a population tested in one year, were calculated. If more than one population of a race was tested, the population averages were in turn averaged to obtain a race average.

The race averages for the fraction of positive results on self-pollination in the pollen tube growth tests and the relative fraction of positive results on self-pollination in the silique growth tests are shown in table 1. The fractions vary from 0.04 to 1.07, but the races fall clearly into two groups. In races c1, c2, c3, c4 and a1 the fractions vary between 0.05 and 0.92, and in at least one of the tests on each of these races there were significantly lower ($P<.01$) fractions of positive results on self-pollination than on cross-pollination. These races may therefore be considered self-incompatible, although the frequency of pseudo-compatibility is sometimes high. In races c5 to c15, a3 and a4, the fractions of positive results on self-pollination are usually between 0.95 and 1.00, although they range from 0.71 to 1.07. There were no significant differences between cross- and self-pollinations in the fractions of positive results in any of the tests on races c5 to c15, a3 and a4, so these populations may be considered self-compatible.

There were no consistent differences between the pollen tube and silique growth tests in the fraction of positive results on self-pollination. This provides additional evidence that the incompatibility barrier in *Leavenworthia* is restricted to the stigma.

The self-incompatible and self-compatible races are clearly separated when the figures for the separate tests on each race are combined as the geometric mean of all tests on the fraction of positive results on self-pollination (table 1). The means of all tests are between 0.17 and 0.54 for the self-incompatible races, and between 0.87 and 1.01 for the self-compatible races. The figure of 0.87 for race a2 is principally due to the failure of self-pollinations (in silique growth tests only) on one of the plants grown in 1963.

In addition, it is apparent that the self-incompatible races differ in the strength of their incompatibility barriers. The means of all tests on races c1, c2 and a1 are less than 0.25, while the means of all tests on races c3 and c4 are slightly greater than 0.50. There is no overlap between the two groups of races in any of the five series of tests, so it is evident that races c1, c2 and a1 have lower frequencies of pseudo-compatibility, *i.e.*, are more strongly self-incompatible, than races c3 and c4.

The fraction of positive results varies considerably in the different series of tests on the same self-compatible race. For example, the five series averages on population 354 (race c2) vary from 0.06 to 0.47. Significant differences between the series of tests were found by χ^2 tests for heterogeneity in populations 171 (race c1), 354 (race c2) and 38 (race c4). These differences are probably due to variations in the environmental conditions in the separate tests. It is well known that the frequency of pseudo-compatibility depends greatly on such factors as the temperature, humidity and the age of the plants (*e.g.*, Lewis, 1943). These factors undoubtedly varied between the separate series and even from day to day in each series.

In most of the self-incompatible populations there were also significant differences between individual plants in the silique growth tests on the fractions of positive results on self-pollination. For example, the results on the six plants of population 171 (race c1) tested in 1962 varied from 0.11 to 0.37. Since the plants were pollinated on the same days, and only healthy plants in mid-flowering were tested, the variation must be due to differences in the strength of the incompatibility reactions in the individual plants.

All of the self-pollinations produced siliques on several plants of self-incompatible populations tested in 1962 and 1963. In each of these cases, however, only twelve or fewer flowers were self-pollinated, and the data are insufficient to distinguish between a high level of pseudo-compatibility and full self-compatibility.

Many of the self-compatible races have gained adaptations to increase the efficiency of self-pollination, such as introrse anthers, have a high spontaneous seed set in the absence of insects and must be largely self-pollinated in nature (see below). But in all races, including the self-compatible ones, fewer seeds are produced in each silique after self-pollination than after cross-pollination (Lloyd, 1964, and unpublished). This is probably due to a low level of inhibition through a self-incompatible reaction which is too weak to prevent the success of self-pollinations, but still operates to restrict the number of seeds after self-pollination.

So it may not be entirely accurate to describe races c5 to c15, a3 and a4 as fully self-compatible. By the usual criteria of equally frequent pollen tube or fruit development after self- and cross-pollination, however, these races would be considered self-compatible, and they will be considered so here. The comparative behavior of cross- and self-pollinations in the races of *L. crassa* and *L. alabamica* will be considered in detail in a later paper.

In summary, four races of *L. crassa* (c1 to c4) and one race of *L. alabamica* (a1) are self-incompatible, with varying degrees of pseudo-compatibility dependent on the particular plant and race tested and the environmental conditions. Self-compatibility has evolved in *L. crassa* (races c5 to c15) and in *L. alabamica* (races a3 and a4). Even in the self-compatible races fewer seeds result, on the average, from self-pollinations than from cross pollinations.

CHARACTERS ASSOCIATED WITH THE EVOLUTION OF SELF-COMPATIBILITY

A considerable number of changes in other characters has accompanied and followed the evolution of self-compatibility in *L. crassa* and *L. alabamica.* Some of these changes have been noted in the genus as a whole (Rollins, 1963). The present discussion is restricted to *L. crassa* and *L. alabamica,* and only racial differences which are associated with the loss of self-incompatibility will be discussed here. The relatively few characters which appear to have evolved independently of the breeding system have been considered in the descriptions of the races.

In the following discussions, an expression of a character is described as primitive if it is usually associated with self-incompatibility, and as advanced if it is found only in self-compatible races. The description of a race as primitive or advanced refers to its overall primitiveness or advancement in characters associated with the breeding system, and is based on the calculation of the advancement indices, discussed below.

The percentage of auto-fertilization: The significance of the presence or absence of self-incompatibility lies in its effect on the frequency of self-fertilization, and thus on the level of heterozygosity and genetic variability in natural populations. The only way in which the relative frequency of self-fertilization in natural populations can be measured directly is by growing and classifying the natural progeny of rare, naturally occurring mutants. This has not been done for the races of *L. crassa* and *L. alabamica,* but a rough indication of the comparative frequencies of self-pollination in the different races can be got from counts of the percentage of fruits in each race which set seed spontaneously under uniform, insect-free conditions in the greenhouse. Accordingly, the number of flowers produced on the plants grown in the greenhouse in 1962 and 1963,

TABLE 2. THE NUMBER OF FLOWERS PER PLANT AND THE PERCENTAGE OF FLOWERS WHICH SET SEED SPONTANEOUSLY (WERE 'AUTO-FERTILIZED') IN A GREENHOUSE IN 1962 AND 1963

Species and Race	Population	No. of plants	Av. no. flowers per plant	Av. no. flowers auto-fert.	Av. % of flowers auto-fert.
		1962			
L. crassa					
Race: c1	171	7	363	4	1
c2	354	10	189	9	5
c3	37	10	208	44	24
c5	58	6	161	77	44
	41	6	150	63	42
	Race average		156	70	43
c6	268	8	101	63	61
c8	72	9	133	88	68
c15	370	3	40	36	91
L. alabamica					
Race: a1	81	5	262	9	4
		1963			
L. crassa					
Race: c1	171	5	465	7	2
c2	354	4	514	11	2
c3	37	6	404	34	8
c4	38	3	447	18	4
c5	86	4	460	40	9
	58	6	295	28	10
	100	8	342	54	18
	41	8	297	25	9
	Race average		349	37	12
c6	268	9	241	38	16
c7	361	7	361	55	15
c8	72	6	225	21	10
c9	769	4	217	22	10
c10	698	10	126	34	30
c11	742	7	163	31	21
c12	739	11	144	34	24
c13	745	9	196	38	20
c14	699	3	115	25	22
c15	370	3	98	31	31
	53	5	122	29	23
	Race average		110	30	27
L. alabamica					
Race: a1	81	2	540	0.5	0.1
	82	4	576	2	0.4
	923	4	394	11	4
	Race average		469	5	2
a2	918	7	297	53	19
a3	275	9	295	40	14
a4	445	2	295	52	18

and the number of flowers which set seed without being manipulated, were counted.

The results (table 2) show that in both 1962 and 1963 there is a clear difference in the percentages of flowers which set seeds spontaneously in self-incompatible and self-compatible populations.

In 1962 the average percentage of flowers which set seed spontaneously ('auto-fertilized' — Drayner, 1959) was 24 per cent or less in the four self-incompatible populations grown, and 42 per cent or more in the five self-compatible populations. The failure of some of the flowers to set seed spontaneously in the self-compatible populations is largely or wholly due to a failure of the pollen grains to be transferred from the anthers to the stigma of the same flower.

In addition, there are conspicuous differences between the self-incompatible populations, and also between the self-compatible populations. In the three populations with relatively strong incompatibility barriers, populations 171 (race c1), 354 (c2) and 81 (a1), 5 per cent or less of the flowers were auto-fertilized, but in population 37 (race c3) which has a weaker self-incompatibility system, 23 per cent of the flowers were auto-fertilized. In the self-compatible populations of races c5, c6 and c8, which have extrorse anthers and petal limbs which bend at right angles to the petal claws in open flowers, between 42 and 68 per cent of the flowers were auto-fertilized. But in population 370 of race c15, 91 per cent of the flowers were auto-fertilized. Race c15 has introrse anthers and semi-erect petal limbs; these characters may increase the possibility that pollen is deposited on the stigma of the same flower.

Plants of at least one population in each of the described races of *L. crassa* and *L. alabamica* were grown in 1963. The results (table 2 & fig. 8) parallel those obtained in 1962, but the percentages of flowers auto-fertilized are consistently lower, particularly for the more advanced races. This is probably due to the fact that the 1963 plants were in general less vigorous, particularly in the later stages of flowering, than the 1962 plants. The amount of auto-fertilization apparently varies considerably within one race and is probably dependent on the vigor of the plants. In 1963 the percentage of auto-fertilization was again consistently higher in the self-compatible populations than in the self-incompatible populations, and almost all of the populations in which more than 20 per cent of the flowers were auto-fertilized have both introrse anthers and semi-erect petal limbs.

The appreciable auto-fertilization in all self-compatible populations under insect-free conditions and in the absence of strong wind currents indicates that these races are well adapted to autogamous reproduction. The percentage of self-fertilization in nature in the races with additional adaptations to facilitate the transfer of pollen from the anthers to the stigma of the same flower might well be as high as 95 or even 99 per cent, since the flowers of these races receive few insect visits (see below).

Inflorescence measurements: The size of the plants of each population grown in the greenhouse in 1962 and 1963 was measured by the number of flowers produced on healthy plants (those with less than 5 per cent of abnormally arrested flowers). The results (table 2 & fig. 9) are given as population and race averages. In those populations for which figures are available from 1962 and 1963, the 1963 figures are considerably higher and in some cases double the 1962 figures. This is perhaps surprising since the 1962 plants were more vigorous in other respects, *e.g.*, average seed weight. The 1963 plants benefited from several improvements in technique, however, and their early growth was superior to that of the 1962 plants. The 1963 plants did not begin to show signs of poor health until after flowering had begun. In addition, the heavier seed set in 1962 by auto-fertilization may have reduced the number of flowers produced that year, particularly in self-compatible populations.

The population averages of the total number of flowers produced on each plant show a reasonably close agreement between the populations of one race, in either 1962 or 1963. The differences between populations of a race are generally small compared with the differences between races and are probably due to differences in the health of the plants of the separate populations.

The race averages show a clear trend of decreasing number of flowers per plant from the most primitive to the most advanced race in both species. Apparently the loss of self-incompatibility has been accompanied by an evolutionary trend toward fewer flowers per plant (under near-optimal conditions). This trend is apparent in the 1962 and 1963 data for *L. crassa* races, and in the 1963 data for *L. alabamica* (only one race of *L. alabamica* was grown in 1962). In both years the most primitive race of *L. crassa* (c1) had more than four times as many flowers per plant on the average as the most advanced race (c15). The difference between the races is not as great in *L. alabamica*, where in 1963 the most primitive race (a1) had an average of almost twice the number of flowers per plant as the most advanced race (a4).

In general, races which are intermediate in the overall advancement in regard to the characters associated with the loss of self-incompatibility have intermediate numbers of flowers, but it is apparent that the order of the plant sizes is not precisely the order of advancement of the races. In 1963 particularly, several races such as c7 and c10 had considerably more or fewer flowers per plant than would be the case if the evolution towards fewer flowers per plant was completely in step with the other characters which have evolved in association with the loss of self-incompatibility.

The production of flowers was analyzed further in the 1963 material by separate counts of the numbers of scapose and branch flowers, and the number of branches produced on each plant (table 3). The results show that the evolution towards fewer flowers per plant has been achieved by a reduction in the number of branch flowers and not by a reduction in the number of scapose flowers. There has been no consistent change at all in the number of scapose flowers in *L. crassa;* there is actually a slight increase in the number of scapose flowers in the more advanced races of *L. alabamica*, but the differences between the races are small compared with the decrease in the number of branch flowers.

The average number of branch flowers can itself be divided into two components — the average number of flowers per branch, and the average number of branches per plant. Table 3 shows that the difference between primitive and advanced races of *L. crassa* and *L. alabamica* in the average number of branch flowers is in turn due to the number of flowers per branch. There is no clear difference between primitive and advanced races in the average number of branches, except that the two most advanced

TABLE 3. BRANCH AND SCAPE MEASUREMENTS AND FLOWER COUNTS ON PLANTS GROWN IN A GREENHOUSE IN 1963

Species and Race	Population	No. of plants	Av. no. of branches per plant	Av. no. of flowers per branch	Av. no. of branch flowers per plant	Av. no. of scapose flowers per plant	Av. total no. of flowers	Av. max. branch length cm	Av. max. scape length cm
L. crassa									
Race: c1	171	5	9.67	41.8	404	60	465	23.5	8.6
c2	354	4	9.71	50.1	486	28	514	26.5	9.1
c3	37	6	8.43	43.6	367	37	404	24.5	8.8
c4	38	3	9.89	41.2	417	31	447	21.3	8.4
c5	86	4	9.00	45.9	413	48	460	30.8	10.2
	58	6	8.71	29.0	253	42	295	21.0	7.6
	100	8	8.10	37.1	300	42	342	21.1	9.0
	41	8	8.38	30.3	254	43	297	23.4	9.2
	Race c5 Average		8.55	35.6	305	44	349	24.1	9.0
c6	268	9	8.09	23.6	191	50	241	16.5	8.3
c7	361	7	12.10	27.7	335	26	361	18.9	6.9
c8	72	6	6.22	28.3	176	48	225	14.0	8.6
c9	769	4	6.17	26.3	163	55	217	15.5	9.9
c10	698	10	6.00	15.6	94	32	126	11.0	10.6
c11	742	7	8.33	16.7	139	24	163	4.1	5.4
c12	739	11	6.36	16.4	104	39	144	7.1	8.2
c13	745	9	9.42	16.1	151	44	196	8.8	6.3
c14	699	3	5.09	15.0	76	39	115	10.2	8.7
c15	370	3	3.00	14.7	44	54	98	6.5	8.3
	53	5	4.50	16.6	75	47	122	7.6	7.5
	Race c15 average		3.75	15.7	60	52	110	7.1	7.9
L. alabamica									
Race: a1	81	2	7.35	69.0	508	32	540	38.0	9.8
	82	4	8.17	65.4	534	42	576	26.6	9.6
	923	4	8.40	43.4	365	29	394	23.2	8.9
	Race a1 Average		7.97	59.3	469	34	503	29.3	9.4
a2	918	1	6.14	40.5	249	48	297	21.6	7.7
a3	275	9	6.64	34.7	231	64	295	18.5	6.7
a4	445	2	7.00	32.6	228	67	295	23.8	7.5

races (c14 and c15) of *L. crassa* have the fewest flowers per branch. It is clear, too, that the large number of flowers per plant in population 361 (race c7) noted above is due to an exceptionally large number of branches per plant.

Apparently the evolution towards fewer flowers per plant in the advanced races of *L. crassa* and *L. alabamica* has been accomplished by a reduction in the number of flowers per branch. There are no races in either species which are conspicuously out of place in this trend, although there is a rather distinct break in *L. crassa* between races c1 to c9, and c10 to c15.

The population averages of the longest branch on each plant in 1963 (table 3, fig. 10) show a reduction in length in the more advanced races of both species, but the trend in this character is not quite as uniform as the trend towards fewer flowers per branch. In particular, race c11 has very short branches, and races c14 and a4 have long branches compared with other advanced races.

The average lengths of the longest scape of the scapose flowers on each plant (table 3) show no consistent differences between advanced and primitive races in either *L. alabamica* or *L. crassa* and are similar in all races except c11, and to a lesser extent c13 and a3, which have unusually short scapes.

The loss of self-incompatibility in *L. crassa* and *L. alabamica* has thus been accompanied by a change in the size of the inflorescences. This has involved a decrease in the number of flowers per branch, and a decrease in the length of the branches, but little or no decrease in the number of branches, the number of scapose flowers, and the length of the scapes. These measurements represent the potentiality of the plants under uniform, near-optimal greenhouse conditions. The plants growing in the glades almost invariably produce fewer branches and flowers. The numbers of branches and of flowers per plant are apparently extremely modifiable, and in nature they are largely controlled by environmental conditions rather than hereditary differences between races.

Flower measurements: A number of measurements were made on flowers collected in the wild in 1962 and from plants grown in the greenhouse in 1963. One flower was removed from each healthy greenhouse plant, and one flower was removed from each of 50 plants of each petal color form present in sufficient frequency in the populations growing in nature. All material was preserved in F.A.A. (90:5:5) and later measured under a dissecting microscope with a micrometer eyepiece. In 1962 the lengths of the petals (claw plus limb), the depth of the emargination of the petal limbs, and the total length of the pistils were measured. In 1963 the same characters plus the length of the ovaries and paired anthers (one of each flower) were measured, and the numbers of ovules and of pollen grains per flower were counted.

The petal and pistil measurements are given in table 4 (1962 field material) and table 5 (1963 greenhouse materi-

TABLE 4. PETAL AND PISTIL MEASUREMENTS ON FLOWERS COLLECTED IN THE WILD IN 1962

Species and Race	Population	Flower color pattern	No. of flowers	Pistil length mm	Petal length mm	Petal emargination depth mm	Nature of site
L. crassa							
Race c1	170	yellow-centered	50	5.34	12.20	1.32	field
	170	yellow	30	5.35	11.83	1.35	field
c2	354	yellow-centered	50	5.45	12.13	0.95	field
	354	yellow	50	5.25	11.46	0.97	field
c3	89	yellow-centered	50	5.97	12.46	1.39	glade
	89	yellow	50	6.34	11.66	1.06	glade
	792	yellow-centered	50	6.52	11.80	0.97	field
	792	yellow	50	7.03	10.93	0.80	field
	Race av.	yellow-centered		6.25	12.13	1.18	
	Race av.	yellow		6.69	11.30	0.93	
c4	66	yellow-centered	50	4.97	11.33	0.91	glade
c5	86	yellow-centered	50	5.91	11.15	1.12	glade
	86	yellow	25	6.04	10.00	0.92	glade
	118	yellow	50	6.09	10.35	0.94	glade
	58	yellow-centered	50	6.22	12.71	1.45	field
	58	yellow	50	6.32	11.17	1.00	field
	100	yellow-centered	50	6.18	12.43	1.47	field
	100	yellow	50	6.25	11.16	1.14	field
	41	yellow	50	5.92	10.08	0.77	field
	Race av.	yellow-centered		6.10	12.10	1.35	
	Race av.	yellow		6.12	10.55	0.95	
c6	268	yellow-centered	50	7.38	11.69	0.91	field
c7	No collection made.						
c8	72	yellow-centered	50	5.16	9.45	0.76	pasture
	72	yellow	50	5.45	8.61	0.44	pasture
c9	No collection made.						
c10	698	yellow-centered	50	5.03	10.03	0.88	glade
	698	yellow	50	5.04	8.93	0.68	glade

c11	No collection made.						
c12	No collection made.						
c13	745	yellow	50	4.93	9.34	0.87	glade
c14	699	yellow-centered	50	5.20	9.97	0.91	glade
c15	53	yellow	50	5.28	10.08	0.44	glade
	27	yellow	50	5.36	9.39	0.43	limestone outcrop
Race av.		yellow		5.32	9.74	0.44	
L. alabamica							
Race a1	923	yellow-centered	50	5.84	11.85	1.00	pasture
a2	No collection made.						
a3	275	yellow-centered	50	5.95	11.94	0.88	field
a4	62	yellow-centered	50	5.59	10.08	0.58	field
	761	yellow-centered	50	5.31	9.71	0.48	forest margin
Race av.		yellow-centered		5.45	9.86	0.53	

al) and shown graphically in figs. 11 to 13. In general, there is a good agreement between the measurements of different populations of one race and between the 1962 and 1963 measurements on flowers of the same race. The samples were taken from plants growing under a wide range of conditions, and some of the populations in the field were in relatively unfavorable sites. The petal and pistil sizes are therefore not very modifiable; even a small plant in nature which produces only one or a few flowers may have normal-sized flowers. In some populations the 1962 field material gave smaller measurements than the 1963 greenhouse plants; in other populations the measurements are larger on the flowers collected in the field.

Several differences between yellow and yellow-centered flowers of the same population were observed, so the measurements are given separately for these two morphs. Yellow-centered flowers have longer petals, deeper petal emarginations and shorter pistils than yellow flowers of the same population in all polymorphic populations measured from both the field and greenhouse collections. Except in population 72 (race c8), the differences between morphs are smaller than the differences between many of the races. The differences between morphs in floral measurements will be considered in a later paper.

TABLE 5. PETAL AND PISTIL MEASUREMENTS ON FLOWERS COLLECTED FROM PLANTS GROWN IN A GREENHOUSE IN 1963

Species and Race	Population	Flower color pattern	No. of flowers	Ovary length mm	Style length mm	Total pistil length mm	Petal length mm	Petal emargination depth mm	Angle between petal claw and limb
L. crassa									
Race: c1	171	yellow-centered	22	2.13	3.70	5.83	12.07	0.97	90°
c2	354	yellow-centered	12	2.31	3.64	5.95	10.94	0.80	90°
c3	37	yellow-centered	16	2.18	3.85	6.03	11.63	0.93	90°
	37	yellow	20	2.18	4.17	6.35	10.47	0.50	90°
c4	38	yellow-centered	14	2.15	3.03	5.18	11.26	0.75	90°
c5	86	yellow	16	1.93	4.47	6.40	10.00	0.79	90°
	118	yellow	8	2.20	3.74	5.94	9.09	0.87	90°
	58	yellow-centered	18	1.92	3.95	5.87	10.12	0.97	90°
	58	yellow	12	2.27	3.91	6.18	10.43	0.96	90°
	100	yellow-centered	20	2.01	3.51	5.52	10.70	1.15	90°
	100	yellow	18	2.43	3.68	6.11	10.58	0.93	90°
	41	yellow	22	2.06	3.64	5.70	9.70	0.92	90°
	Race[1] av.	yellow-centered		1.97	3.73	5.70	10.41	1.06	90°
	Race av.	yellow		2.18	3.89	6.07	9.96	0.89	90°
c6	268	yellow-centered	22	2.35	4.55	6.90	10.21	0.85	90°
c7	361	yellow-centered	20	2.02	2.21	4.23	10.33	0.90	90°
c8	72	yellow-centered	18	2.18	3.21	5.39	10.78	0.69	90°
	72	yellow	14	1.95	3.57	5.52	8.73	0.42	90°
c9	769	yellow-centered	22	2.14	2.53	4.67	9.77	1.06	90°
c10	698	yellow-centered	20	1.81	3.29	5.10	10.02	0.61	<90°
c11	742	yellow-centered	20	1.77	2.68	4.45	9.56	0.71	<90°
c12	739	yellow	18	1.94	2.61	4.55	7.81	0.44	≥90°
c13	745	yellow	20	2.10	3.19	5.29	9.52	0.82	<90°
c14	699	yellow-centered	4	1.80	3.20	5.00	8.13	0.47	<90°
c15	370	yellow	18	2.22	2.47	4.69	8.77	0.27	<90°
	53	yellow	14	2.23	2.53	4.76	8.67	0.43	<90°
	750	yellow	8	2.00	2.50	4.50	8.63	0.34	<90°
	Race av.	yellow		2.15	2.50	4.65	8.69	0.35	<90°
L. alabamica									
Race a1	81	yellow-centered	10	3.27	2.76	6.03	12.88	1.17	90°
	82	yellow-centered	18	3.40	2.31	5.71	12.54	1.05	90°
	923	yellow-centered	20	2.86	2.24	5.10	12.45	1.06	90°

Race	av.	yellow-centered		3.18	2.44	5.61	12.62	1.09	90°
a2	918	yellow-centered	16	4.06	2.56	6.62	12.06	0.88	90°
a3	275	yellow-centered	16	3.10	2.65	5.75	11.19	1.02	90°
a4	445	yellow-centered	18	3.28	1.98	5.26	9.26	0.33	<90°

[1] The race averages are the arithmetic means of the population averages.

The average petal lengths, like many other characters, show a trend from the more primitive to the more advanced races in both *L. crassa* and *L. alabamica,* with the primitive races having longer petals. However, the order of decreasing length is not exactly the order of increasing advancement of the races; for example, race c12 and not race c15 has the shortest petals of any *L. crassa* race.

The average petal emarginations also show a general difference between the primitive and advanced races in both species — the primitive races having deeper emarginations than the advanced races of the same species. The evolution towards shallower petal emarginations that has accompanied the evolution of self-compatibility has not always been completely in step with other morphological changes. In particular, population 769 (race c9) has deeper petal emarginations than other advanced races of *L. crassa.*

The pistil lengths are generally greater in the primitive races of *L. crassa* and *L. alabamica* than in the advanced races. In this character races c4 and c7 have lower measurements than the races closest to them in the sequence of races in *L. crassa.* Races c6 and a2 have the longest pistils in *L. crassa* and *L. alabamica* respectively.

The average ovary lengths and style lengths (which together make up the pistil lengths) in the greenhouse measurements show that the evolutionary trend in the pistil length is due entirely to a trend in the style length. There is no consistent difference between primitive and advanced races in either *L. crassa* or *L. alabamica* in the length of the ovaries. There is, however, a general difference in the length of the ovaries between *L. crassa* and *L. alabamica.* The longest ovaries in *L. crassa* do not exceed 2.5 mm (the highest race average is 2.31 mm for race c2), but the ovaries are always longer than 2.5 mm in *L. alabamica* (the lowest race average in *L. alabamica* is 3.18 mm). In spite of this, the pistil lengths are very similar in *L. crassa* and *L. alabamica,* since the styles are much shorter in *L. alabamica.* The resulting uniformity in *Leavenworthia* in the relative positions of the stigma, anthers and petal limbs is presumably an adaptation to a uniform method of pollination (see below).

The average lengths of the paired anthers on the flowers collected in the greenhouse are shown in table 6. There is again a difference between the primitive and advanced races in both species, with the primitive races having longer anthers than the advanced races. Moreover, races a1 and a2 of *L. alabamica* have longer anthers than any of the races of *L. crassa.*

Number of ovules per flower: In 1963 the number of ovules was counted in each of the flowers from which petal and pistil measurements were taken. The results (table 6) show that there is no general difference between self-incompatible and self-compatible races in either *L. crassa* or *L. alabamica.* The number of ovules per flower varied considerably in each population, and this is shown in table 6 by the range in ovule numbers per flower in each population. Apparently the number of ovules in a flower is very modifiable and depends to a considerable extent on the vigor of the plant concerned. In general the flowers of *L. crassa* have fewer ovules per flower than the flowers of *L. alabamica* (cf. Rollins, 1963). Although there is a considerable overlap in the figures for the two species in table 6, the fruits of all races of *L. alabamica* in nature often have more than twelve seeds per fruit, while those of *L. crassa* usually have less than ten seeds per fruit. The difference between the species has been partially obscured in the ovule counts on greenhouse material due to the fact that the conditions were not optimal.

It is not surprising that the ovary lengths and the number of ovules per flower show similar patterns of variation. Neither differs consistently between the primitive and advanced races of *L. crassa* and *L. alabamica,* but in both there is a difference between the species.

The pollen:ovule index: The average number of pollen grains in a flower was measured for each of the populations grown in 1963 by suspending all of the pollen grains from five flowers (from five different plants) in 0.4 ml of a solution containing three parts of lactic acid to one part of glycerine and shaking the suspension for 30 seconds against a Vortex Junior Mixer. A small sample was removed with a dropper and placed on a haemocytometer slide. When the coverslip was put over this suspension the volume of liquid between the coverslip and each of the two grids marked on the slide was exactly 0.0001 cc. The pollen grains within each grid were counted and the procedure repeated, so that four counts of the number of pollen grains in 0.0001 cc of liquid were obtained. The use of a viscous medium only slightly less dense than the pollen grains ensured that the pollen grains did not move towards the margin of the coverslip but remained uniformly suspended throughout the medium. The average number of pollen grains in each of the five flowers sampled is then:

$$\frac{\text{the total number of grains counted in 4 samples}}{\text{4 (number of samples)} \times \text{5 (number of flowers)}} \times \frac{\text{0.4 (ml)}}{\text{0.0001 (cc)}}$$

$$\textit{i.e.}, \text{ total count} \times 200$$

The results of the counts on each population are shown in table 6. In both *L. crassa* and *L. alabamica* the number of pollen grains per flower in the most primitive races (c1 and a1 respectively) is more than twice as great as the number in the most advanced race of the same species (c15 and a4 respectively). Intermediate races have intermediate numbers of pollen grains per flower in general, although race c13 of *L. crassa* has somewhat fewer pollen grains per flower than race c15. As one would expect, there is a close similarity in the variations between the species and races in the average lengths of the paired anthers discussed previously and the average number of pollen grains in each flower.

In itself the number of pollen grains per flower is not very meaningful; the important biological parameter is the number of pollen grains per flower divided by the number of ovules per flower. This is given in table 6 and fig. 14 as the pollen:ovule index, and measures the average number of pollen grains available for each ovule. Since the differences between races of one species in the number of ovules per flower are generally small, the pollen:ovule indices show differences within each species similar to that in the number of pollen grains per flower, *i.e.*, an evolutionary

TABLE 6. ANTHER MEASUREMENTS AND POLLEN AND OVULE COUNTS ON FLOWERS COLLECTED FROM PLANTS GROWN IN A GREENHOUSE IN 1963[1]

Species and Race	Population	Flower color pattern	Av. no. of ovules per flower	Range of no. of ovules per flower	Anther length mm	Total no. of pollen grains counted	No. of pollen grains per flower × 1000	Pollen: ovule index[2]	Angle rotated by anthers
L. crassa									
Race: c1	171	yellow-centered	5.94	4- 8	1.81	272	54.4	9160	135-225°
c2	354	yellow-centered	6.73	5- 8	1.75	148	30.0	4400	135-180°
c3	37	yellow-centered	7.67	6-11	1.87	265	53.0	6910	135-180°
	37	yellow	8.67	6-10	1.86	219	43.8	5050	135-180°
c4	38	yellow-centered	6.00	5- 8	1.65	172	34.4	5730	135-180°
c5	86	yellow	7.00	6- 9	1.55	158	31.6	4510	135-180°
	118	yellow	7.25	5- 8	1.51	199	39.8	5490	135-180°
	58	yellow-centered	7.13	5- 9	1.66	158	31.6	4430	135-180°
	58	yellow	6.75	5- 8	1.67	147	29.4	4360	135-180°
	100	yellow-centered	8.81	6-14	1.82	187	37.4	4250	135-180°
	100	yellow	8.84	6-11	1.82	175	35.0	3960	135-180°
	41	yellow	8.30	6-11	1.81	211	42.2	5080	135-180°
	Race av.	yellow-centered	7.97		1.74	173	34.6	4340	135-180°
	Race av.	yellow	7.63		1.67	178	35.6	4680	135-180°
c6	268	yellow-centered	9.38	7-12	1.64	170	34.0	3620	135-180°
c7	361	yellow-centered	7.09	4- 9	1.42	146	29.2	4120	135° or less
c8	72	yellow-centered	9.10	8-11	1.63	205	41.0	4510	135-180°
	72	yellow	7.50	6-10	1.63	126	25.2	3360	135-180°

c9	769	yellow-centered	8.77	6-12	1.60	156	31.2	3560	180-225°
c10	698	yellow-centered	7.20	4-10	1.38	133	26.6	3690	90-135°
c11	742	yellow-centered	6.90	6- 9	1.40	135	27.0	3910	135-180°
c12	739	yellow	7.25	4- 9	1.50	142	28.4	3920	135-180°
c13	745	yellow	6.05	4- 8	1.43	98	19.6	3240	90°
c14	699	yellow-centered	6.75	6- 8	1.23	120	24.0	3480	90-135°
c15	370	yellow	6.62	5- 8	1.68	116	23.2	3500	90°
	53	yellow	7.75	7- 9	1.47	95	19.0	2450	90°
	750	yellow	7.40	4- 9	1.47	114	22.8	3080	90°
	Race av.	yellow	7.26		1.51	108	21.6	3010	90°
L. alabamica									
Race: a1	81	yellow-centered	11.40	10-15	2.03	377	75.4	6610	135-180°
	82	yellow-centered	12.00	10-17	2.15	362	72.4	6030	135-180°
	923	yellow-centered	8.78	7-13	2.07	371	74.2	8450	135-180°
	Race av.	yellow-centered	10.79		2.08	370	74.0	7030	135-180°
a2	918	yellow-centered	10.44	9-13	1.94	218	43.6	4180	135-180°
a3	275	yellow-centered	7.65	6- 9	1.61	158	31.6	4130	135-180°
a4	445	yellow-centered	8.95	8-11	1.44	129	24.8	2770	90°

[1] The ovule counts and anther length measurements were made on the same flowers used for the petal and pistil measurements (table 5).

[2] The pollen:ovule index is the estimated number of pollen grains per flower divided by the average number of ovules per flower.

trend towards a decrease of the pollen:ovule index has accompanied the evolution of self-compatibility in both *L. crassa* and *L. alabamica.*

Nectar guides: At the base of the petal limbs of all races there are three lines radiating from the middle of the petal towards the distal end of the limb (fig. 3). The lines are composed of superimposed orange and brown pigments and presumably serve as nectar-guides to direct insects to the pollen and nectar supplies (Manning, 1956). In most races the orange pigment predominates, and the nectar guides contrast strongly with the yellow background of the petal limbs. But in the self-compatible races c10, c11 and c14 the orange pigment is masked by the brown pigment, and the nectar guides are less conspicuous.

Flower color pattern: All of the races of *L. crassa* and *L. alabamica,* except races c12, c13 and c15, have some or all plants with yellow-centered flowers. In most races the yellow 'eye' of yellow-centered flowers is quite bright and ends abruptly, so there is a strong contrast between the yellow and white portions of the petal limbs (fig. 3). But in races c10 and c14 the yellow 'eye' is less well defined and not as bright as in other races, so that it contrasts less strongly with the distal white portions of the petals.

Angle rotated by the anthers: The anthers of the paired stamens face directly towards the pistil in the developing bud (position 0° in fig. 6). During the opening of the flower the filaments of the paired anthers slowly turn, so that the anthers are rotated to a degree characteristic of each race. The anthers of the single stamens do not rotate, so that the pollen is exposed towards the pistil, and the single anthers are always introrse. The anthers of the paired stamens of the self-incompatible races and some self-compatible races rotate through 135° to 180° and are extrorse in the open flower (table 6). The anthers of races c1 and c9 may rotate up to 225°. In the self-compatible races c13, c15 and a4 the anthers of the paired stamens rotate through approximately 90° (or less in dull weather) and remain more or less introrse. Races c7, c10 and c14 are intermediate in this regard, and different anthers, even on the same flower, may be introrse or extrorse.

Silique measurements: Several measurements were made on mature siliques collected in the field in 1962 and in the

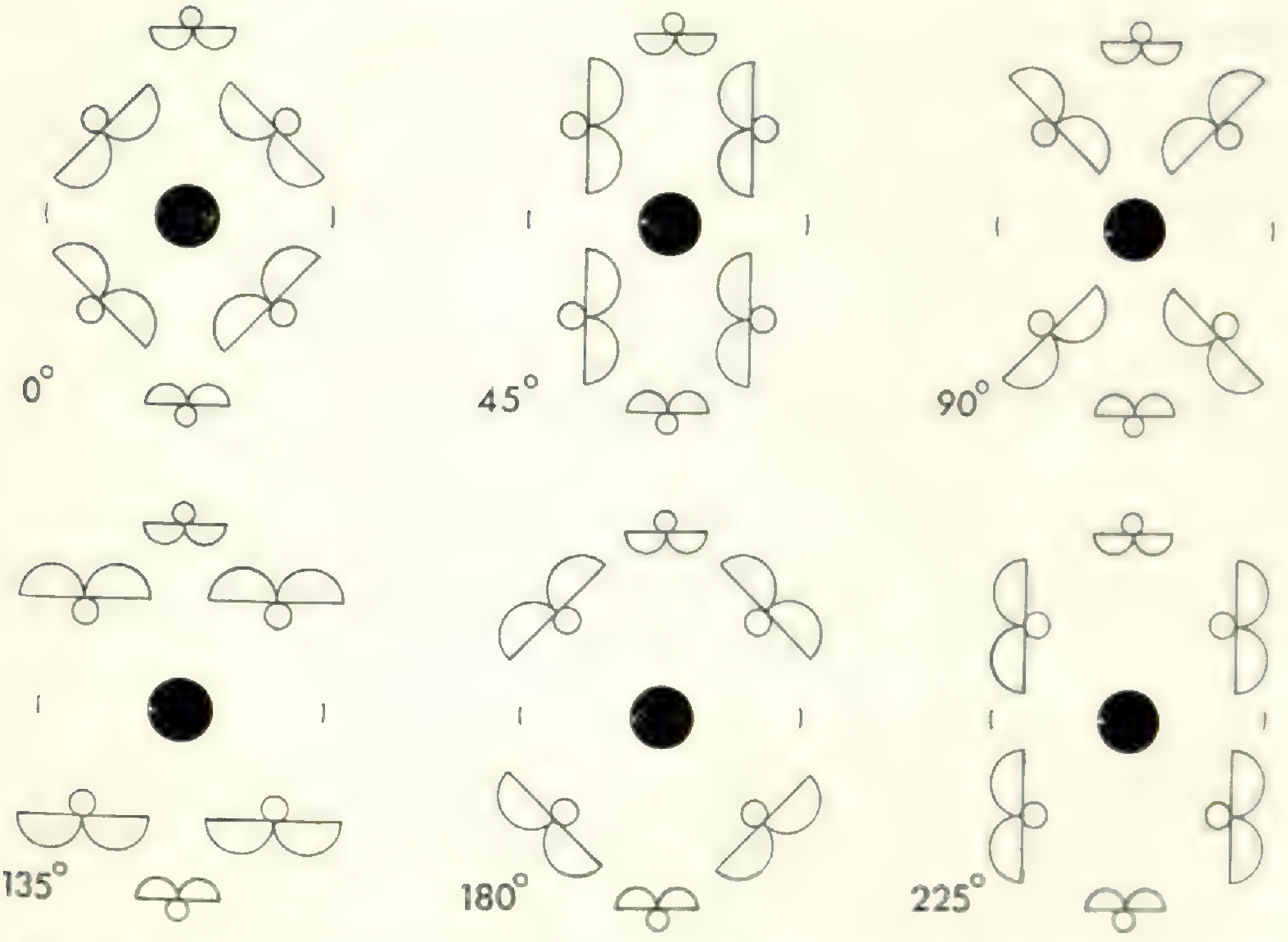


FIG. 6. Diagram of the anther positions corresponding to the various angles through which the anthers of the paired stamens rotate. The stigma at center is black. The anthers of the single stamens are most remote from the stigma and are smaller than the anthers of the paired stamens. The dehiscence lines of the anthers are on the rounded portion of each anther sac. The pairs of stamens are indicated by small brackets. Positions 0° to 90° are described as introrse; positions 135° to 225° are described as extrorse.

greenhouse in 1962 and 1963 (table 7). The length of the siliques is very variable in most populations, both in the greenhouse and in nature. Like the number of flowers per plant, the number of ovules per flower and the weight of seeds, the length of the siliques on a plant is apparently very dependent on the environmental conditions under which the plant is growing. In nature, particularly in cedar glades, conditions become unfavorable for *Leavenworthia* later in the flowering season, and silique growth is arrested. The length of a silique depends largely on the growth accomplished before the glade soil becomes too dry. The 1963 greenhouse plants (and to a less extent the 1962 greenhouse plants) became unhealthy later in the flowering period, and many siliques did not attain the size they would have reached under perfect conditions. For these reasons the maximum, rather than average, silique lengths and widths in each population are given for both the field and greenhouse collections. Where siliques were collected from one population in the greenhouse in both 1962 and 1963, the measurements given are the greater of the two measurements for each year. No attempt was made to distinguish between the silique lengths of the morphs in polymorphic populations.

The maximum silique lengths of all races of *L. crassa* are less than 13 mm, but the maximum silique lengths of all

TABLE 7. SILIQUE MEASUREMENTS AND SEED WEIGHTS[1]

Species and Race	Population	Maximum silique length mm		Maximum silique width mm		Av. seed weight mg.
		Field	Greenhouse	Field	Greenhouse	Greenhouse
L. crassa						
Race: c1	171	12.1	14.8	4.3	4.3	1.71
c2	354	9.9	13.1	4.9	4.9	1.94
c3	37	7.6	12.7	5.4	5.6	1.68
	743	7.4	—	5.5	—	—
c4	38	9.4	—	5.2	—	—
c5	86	7.4	8.6	5.0	5.2	—
	118	8.9	9.4	4.8	4.5	—
	58	9.3	10.5	4.9	5.1	1.64
	100	8.3	10.2	5.3	4.9	—
	41	9.6	11.3	5.4	5.5	—
c6	268	9.8	11.0	5.0	4.7	1.57
c7	361	9.1	9.3	4.8	4.3	—
c8	72	7.7	8.8	4.5	5.0	1.28
c9	769	9.7	8.1	5.4	5.1	—
c10	698	6.5	9.4	5.0	4.4	—
c11	742	8.4	8.8	4.4	4.2	—
c12	739	9.2	8.7	5.4	5.1	—
c13	745	9.2	8.3	4.8	4.4	—
c14	699	9.9	—	4.7	—	—
c15	370	10.2	11.6	5.1	5.4	1.21
	53	10.6	10.6	4.9	4.8	—
	750	10.1	9.6	4.8	4.8	—
L. alabamica						
Race: a1	81	26.7	20.0	4.4	4.0	—
	82	30.0	21.8	3.7	3.4	—
	923	19.2	17.6	4.4	3.6	—
a2	918	27.9	19.7	4.9	3.4	—
a3	275	23.4	19.0	3.7	4.6	—
a4	445	17.6	15.1	4.2	3.4	—

[1] The figures for the greenhouse collections are those of the 1962 and 1963 collections considered together. The seed weights are those from cross-pollinations on the 1962 greenhouse material.

races of *L. alabamica* are more than 17 mm. Rollins (1963) observed a similar difference between the species in average silique lengths from field collections. As noted previously, similar differences in the ovary lengths in the two species are already apparent in the flowers before they are pollinated.

In addition, the best-developed siliques of the primitive races of each species are generally longer than the best-developed siliques of the advanced races of the same species. The differences within *L. crassa* are not very great, and on the basis of the material available it is only certain that under optimal conditions race c1 has the longest siliques, races c2 and c3 have somewhat shorter siliques, and the remaining, more advanced, races have still shorter siliques. The field and greenhouse measurements on three populations of race c15 are all greater than those on races c7 to c14, and it is probable that race c15 has longer siliques under optimal conditions than races c7 to c14. In *L. alabamica*, races a1 and a2 have greater maximum silique lengths than races a3 and a4. Observations in the field also show that the siliques of races a3 and a4 are shorter than those of races a1 and a2.

Rollins (1963) did not obtain any consistent difference between the average silique lengths of field collections of *L. alabamica* var. *alabamica* and *L. alabamica* var. *brachystyla* (race a4 of the present paper) or between *L. crassa* var. *crassa* and *L. crassa* var. *elongata* (race c15 of the present paper). Most of the average measurements he obtained are considerably less than the maximum measurements I obtained, and they may not reflect the genetical potentialities of the populations measured.

There is much less variation between species, races and collections in the maximum silique widths than in the maximum silique lengths (table 7). Siliques which develop any viable seeds at all generally have widths approaching the maximum width of the population to which they belong, although their lengths may be less than half the maximum. The data suggest that the siliques of *L. alabamica*, and of races c1 and c11 of *L. crassa*, are narrower than those of other races of *L. crassa*, and that there is no consistent difference between self-incompatible and self-compatible races. Rollins (1963) also obtained smaller silique width measurements in *L. alabamica* than in *L. crassa*.

Seed weight: There is some evidence that a trend towards a decrease in the average weight of seeds has accompanied the evolution of self-compatibility. The seeds produced from controlled pollinations in the greenhouse in 1962 and 1963 were weighed, and race averages were obtained. The average seed weights of the three self-incompatible races of *L. crassa* grown in 1962 exceeded the average seed weights of the four self-compatible populations, and within the self-compatible populations the order of decreasing seed weights corresponds with increasing advancement in characters associated with the evolution of self-compatibility (table 7). The seed weights obtained in 1963 were all considerably below the 1962 figures due to the plants being less vigorous, so it was not possible to compare the potentialities of the different races from this material. The evidence for a trend towards lighter seeds in more advanced races thus rests on the 1962 measurements on seven *L. crassa* races.

Discussion: So far, it has been shown that there is a whole complex of changes which have accompanied or followed the loss of self-incompatibility in *L. crassa* and *L. alabamica.* It should be pointed out that the measurements discussed were largely taken from plants growing in the greenhouse. Some of the characters, particularly the number of flowers per plant, are very modifiable, and measurements of these characters depend greatly on the conditions under which a plant is growing. The differences between primitive and advanced races are greatest under optimal conditions and are less obvious in plants growing in nature under very variable conditions.

The following is a list of the changes which have accompanied or followed the loss of self-incompatibility in some or all of the self-compatible races of *L. crassa* and *L. alabamica.*

1. An increase in the percentage of flowers auto-fertilized in the greenhouse. Presumably this has enabled an increase in autogamous reproduction in nature.
2. A decrease in the number of flowers produced under optimal conditions.
3. A decrease in the length of branches under optimal conditions.
4. A decrease in petal length.
5. A decrease in the depth of petal emarginations.
6. A decrease in the contrast between the (proximal) yellow and (distal) white portions of yellow-centered flowers.

7. A decrease in the brightness of the nectar-guides.
8. A change from horizontal to sub-erect petal limbs.
9. A change from extrorse to introrse anthers (paired stamens).
10. A decrease in anther length (paired stamens only measured). This is associated with a decrease in the number of pollen grains per flowers, and in the pollen:ovule index.
11. A decrease in pistil length, due to a decrease in style length.
12. A decrease in silique length.
13. A decrease in the weight of individual seeds. (The evidence for this is incomplete.)

The list is not exhaustive. Several characters which were not measured could probably be added. For example, Rollins (1963) showed that the self-compatible species of *Leavenworthia* have shorter sepals than the self-incompatible species. The length of the sepals and the length of the stamen filaments appear to vary with the length of the pistil. Observations on the plants grown in the greenhouse indicate that decreases in the number and length of the leaves have occurred in some of the more advanced races of *L. crassa* and *L. alabamica.* Both of these characters are very variable in a population (and the leaves on a single plant vary greatly in length), and detailed measurements of them were not made. However, the more extreme differences between races in the length of the leaves are indicated above in the descriptions of the races.

The above list agrees in general with that given in Rollins (1963) for evolutionary trends in the genus as a whole, though there are some differences in the two lists. Several of the characters which I have measured have not been studied in other species of *Leavenworthia*, and the trends noted in these characters may not apply to the other species.

Three of the trends given by Rollins do not apply to *L. crassa* and *L. alabamica.* None of the races of *L. crassa* or *L. alabamica* has evolved as far towards complete autogamy as the self-compatible species *L. exigua*, *L. torulosa* and *L. uniflora.* For example, all the races of *L. crassa* and *L. alabamica* have remained odoriferous, whereas *L. aurea*, *L. exigua, L. uniflora* and some populations of *L. torulosa* have become non-odoriferous. There has been no increase in ovule number in the advanced races of *L. crassa* or *L. alabamica* comparable to the increase in *L. uniflora* when compared with other species of the genus. Rollins (1963) noted that the self-compatible species of *Leavenworthia* have larger stigmas than the self-incompatible species. There is no such difference between self-compatible and self-incompatible races of *L. crassa* and *L. alabamica;* all races have stigmas *ca.* 0.5 mm wide.

The changes which have accompanied and followed the loss of self-incompatibility may be considered under three headings: those which have resulted in an increased efficiency in self-pollination, those which may be considered as losses of adaptations to insect pollination, and those which appear to be responses to the conditions under which self-compatible races grow. The selective forces responsible for the changes are inter-related and the three groups are not mutually exclusive.

The loss of self-incompatibility in some races of *L. crassa* and *L. alabamica* has itself made self-pollination easier and more frequent, as the figures on auto-fertilization show. Self-compatible races vary in the amount of auto-fertilization, and it is clear that other floral characters also influence the amount of auto-fertilization. The most important of these is probably the evolution of introrse paired anthers in some of the advanced races. The relative heights of the style and the anthers of paired stamens and the closing of the petals in the late afternoon may also influence the amount of auto-fertilization. The trends towards decreases in the anther lengths and pollen:ovule indices perhaps reflect an increased efficiency in (self-) pollination in these races (cf. Darwin, 1876, p. 386).

Many of the changes associated with the loss of self-incompatibility may be regarded as losses of adaptations to insect visitors. This does not imply that such changes have occurred as a result of selective forces favoring fewer insect visits in self-compatible races. On the contrary, the large number of adaptations to insect visitors retained in many of the self-compatible races suggests that these races still rely to a considerable extent on cross-pollination (cf. Darwin, *loc. cit.*). It will be shown below that flowers of self-compatible races are visited by insects, though less often than flowers of self-incompatible races. Perhaps the partial loss of adaptations to insect pollination should be regarded as 'economy measures' adopted in the relatively unfavorable habitats of the self-compatible races, where growth is poorer, and seed production is curtailed by the drying of the soils.

The decrease in the petal lengths, the change from horizontal to sub-erect petal limbs, the decrease in the contrast between the yellow and white portions of yellow-centered flowers, and the decrease in the brightness of nectar-guides in some self-compatible races have all reduced the conspicuousness of the flowers, at least to the human eye. The pistil length is probably largely determined by natural selection controlling the depth of concealment of the nectaries. This depth is determined by the length of the petal claws, since the stigma and the anthers of paired stamens are at, or slightly above, the level of the outspread petal limbs. Apparently there has been a trend towards decreasing the depth of concealment of the nectaries, and this is reflected in the decrease in the length of the styles.

The significance of the decrease in the length of the petal emarginations in the advanced races is uncertain. The researches of Hertz, von Frisch and Kugler have shown that honeybees and bumblebees are attracted more frequently to experimental models with more complicated outlines. They apparently recognize the degree of 'brokenness' of an object, rather than its total form (von Frisch, 1950; Free and Butler, 1959). The emarginations of the petal limbs in *Leavenworthia* may serve to make the flowers more visible to the bees which pollinate them and may be deeper in the regularly cross-pollinated, primitive races for this reason.

The trends towards decreases in the length of branches, the number of flowers, the silique lengths and the weight of seeds cannot be explained as either losses of adaptations to insect visitors or adaptations increasing the efficiency of autogamous reproduction. They may reflect a reduced growth potential in the advanced races of *L. crassa* and *L. alabamica*. It will be argued below that the self-compatible races exist on drier, less favorable glade sites and have evolved under these conditions.

THE CALCULATION OF AN ADVANCEMENT INDEX FOR EACH RACE

So far I have considered the evolution of characters associated with the loss of self-incompatibility individually as though they were completely independent of one another. But it is apparent that in general if a race is primitive in one of these characters, it is more or less primitive in the others. Similarly, some races are more or less advanced in all characters associated with the change in the breeding system. Thus some races, particularly self-incompatible ones, may be described as relatively primitive; other races are in general relatively advanced. The description of a race as primitive or advanced refers here only to the sum total of the expressions of the characters associated with the evolution of self-compatibility, and does not take into account racial differences which are not associated with the evolution of self-compatibility.

A measure of the total evolution towards increasing autogamy has been obtained by considering ten of the fourteen associated changes together in one index. The ten changes (including the weakening and loss of self-incompatibility itself) which were most fully documented and showed the most consistent differences between self-incompatible and self-compatible races were chosen for this index.

The index is based entirely on the 1963 greenhouse measurements, except for the race averages of the fraction of positive results on self-pollination, which are geometric means of all pollen-tube and silique growth tests on a race. The field measurements and the 1962 greenhouse measurements did not include every race and were therefore excluded. Besides, field measurements of highly modifiable characters, such as the number of flowers per plant, do not reflect the genetic potentiality of the plants and would be quite misleading.

To construct the index measuring the advancement of each race in the characters associated with the evolution of self-compatibility, the range of measurements in each of the ten chosen characters was grouped into three classes (except for the angle between the petal claw and petal limb, which was divided into two classes). The class limits for each character (table 8) were chosen (a) to divide the range of the race averages for each measurement as nearly as possible into three equal classes, and (b) as numbers as rounded off as possible, *e.g.*, 10 and 20 cms for the average maximum branch lengths. The class which includes the most primitive expressions of each character was then given a score of 0, the class which includes the intermediate measurements of each character was given a score of 5, and the class which includes the most advanced expressions of each character was given a score of 10.

For every race of *L. crassa* and *L. alabamica*, the race average for each of the ten measurements was then given a score corresponding to that of the class into which it fell. For example, the average maximum branch length in race c1 was 23.5 cm; since this is greater than 20.0 cm, it is classed as primitive and is given a score of 0. It was pointed out previously that the petal color morphs of one population differ considerably in several characters. The morphs in the polymorphic races are accordingly given separate scores for characters 3, 4, 7, and 8 in table 9.

The score (or scores in polymorphic populations) for each character and for all races of *L. crassa* and *L. alabamica* is given in table 9. The total of the scores for the ten characters in each race is given on the right-hand side of the table. In polymorphic races, the separate totals for the morphs are given, and the race total is taken as the average of the morph totals.

I have called the total scores for each race 'advancement indices' — a term used by Sporne (1956) in describing the evolution of Angiosperm families. The advancement indices of the races may, and in fact do, vary between 0 (primitive in all ten characters) and 100 (advanced in all characters). Two self-incompatible races (c1 of *L. crassa* and a1 of *L. alabamica*) have advancement indices of 0. The remaining self-incompatible races, c2, c3 and c4 have advancement indices between 5 and 15. The self-compatible races of *L. crassa* have advancement indices between 22.5 and 100; the self-compatible races of *L. alabamica* have advancement indices between 25 and 70.

The advancement indices provide the basis for the naming of the races of *L. crassa* and *L. alabamica*. The races in each species have been numbered in the order of increasing advancement indices. Each race is then designated by the first letter (in lower-case type) of the species to which it belongs, followed by the rank of the race in the species. Thus the most primitive race of *L. crassa* is race c1, and the most primitive race of *L. alabamica* is race a1, etc.

Two races in *L. crassa* have identical advancement indi-

TABLE 8. CLASS LIMITS AND CLASS SCORES FOR ALL CHARACTERS CONTRIBUTING TO THE ADVANCEMENT INDICES

Class	Class Score	Characters and class limits									
		Av. max. branch length cm.	Av. no. of flowers	Av. petal length mm.	Av. petal emargination depth mm.	Angle between petal claw and limb	Angle rotated by stamen filaments	Av. pistil length mm.	pollen: ovule index	Av. fraction of positive results on self-pollination	Av. % of flowers auto-fertilized
		1	2	3	4	5	6	7	8	9	10
Primitive	0	≥20.0	≥300	≥10.00	≥0.75	90°	≥135°	≥5.50	≥6000	0.00-0.33	<10
Intermediate	5	10.0-19.9	200-299	9.00-9.99	0.50-0.75	—	90°-135°	5.00-5.4°	4000-5999	0.33-0.66	10-19
Advanced	10	<10.0	<200	< 9.00	<0.50	<90°	90°	<5.00	<4000	0.67-1.00	≥20

TABLE 9. CALCULATIONS OF THE ADVANCEMENT INDICES FOR ALL RECOGNISED RACES OF L. CRASSA AND L. ALABAMICA[1]

Species and Race	Flower color morph (s)	Characters and scores										Advancement Indices (total scores)	
		1	2	3	4	5	6	7	8	9	10	Morph total	Av. race total
L. crassa													
Race: c1	yellow-centered	0	0	0	0	0	0	0	0	0	0	0	0
c2	yellow-centered	0	0	0	0	0	0	0	5	0	0	5	5
c3	yellow-centered, yellow	0	0	0,0	0,5	0	0	0,0	0,5	5	0	5,15	10

c4	yellow-centered	0	0	0	0	0	0	5	5	5	0	15	15
c5	yellow-centered, yellow	0	0	0,5	0,0	0	0	0,0	5,5	10	5	20,25	22.5
c6	yellow-centered	5	5	0	0	0	0	0	5	10	5	30	30
c7	yellow-centered	5	0	0	0	0	5	10	5	10	5	40	40
c8	yellow-centered, yellow	5	5	0,10	5,10	0	0	5,0	5,10	10	5	40,55	47.5
c9	yellow-centered	5	5	5	0	0	0	10	10	10	5	50	50
c10	yellow-centered	5	10	0	5	10	5	5	10	10	10	70	70
c11	yellow-centered	10	10	5	5	10	0	5	10	10	10	75	75
c12	yellow	10	10	10	10	0	0	10	10	10	10	80	80
c13	yellow	10	10	5	0	10	10	5	10	10	10	80	80
c14	yellow-centered	5	10	10	5	10	5	10	10	10	10	85	85
c15	yellow	10	10	10	10	10	10	10	10	10	10	100	100
L. alabamica													
Race: a1	yellow-centered	0	0	0	0	0	0	0	0	0	0	0	0
a2	yellow-centered	0	5	0	0	0	0	0	5	10	5	25	25
a3	yellow-centered	5	5	0	0	0	0	0	5	10	5	30	30
a4	yellow-centered	0	5	5	10	10	10	5	10	10	5	70	70

[1] The characters are numbered as in table 8. The class limits and class scores are given in table 8. For the polymorphic races c3, c5 and c8, the scores are given separately in columns 3, 4, 7 and 8 for both flower color morphs, in the order shown at left.

ces. Races c12 and c13 both have advancement indices of 80; race c12 has extrorse anthers, and has therefore been ranked ahead of race c13, which has introrse anthers and may be more frequently self-pollinated.

The advancement indices indicate roughly how far each race has evolved in the characters associated with the evolution of self-compatibility. It is apparent from table 9 that the races of *L. crassa* and *L. alabamica* show a wide variety in the extent to which they have evolved in these characters. The advancement indices probably also broadly parallel the percentage of self-pollination in each race; the correspondence will not be perfect, however, since some of the characters contributing to the advancement indices do not directly affect the ease of self-pollination, while others have a strong effect.

THE PATTERN OF EVOLUTION OF CHARACTERS ASSOCIATED WITH THE EVOLUTION OF SELF-COMPATIBILITY

The discussion of the individual characters associated with the loss of self-incompatibility emphasized that the order of increasing advancement in the various characters often did not correspond exactly. Apparently the evolution of these characters has not followed a completely constant pattern. For example, race c15 is the most advanced race of either species when all characters are considered, but it is *the* most advanced race in only a few of the single characters. In race c7 the pistil is shorter than in any other race of either *L. crassa* or *L. alabamica,* yet overall this race is only moderately advanced. Similarly race c11, and not race c15, has the shortest (most advanced) branches of any race of either species, race c12 has the shortest petals, etc.

There is nevertheless a strong parallel in the evolution of these characters in each race, and the pattern of gain of advanced characters seems to be fixed to some extent. The most advanced races in both *L. crassa* and *L. alabamica* are moderately to highly advanced in all characters. And the most primitive self-compatible races (c5, c6 and a2) are similar to the self-incompatible races in all characters.

The degree of constancy in the pattern of evolution of advanced characters may be seen best when the measurements obtained on each race for a given character are plotted against the advancement index of the race concerned.

The resulting graphs are shown in figs. 7 to 14 for the ten characters which contribute to the advancement indices. The two semi-quantitative characters, the degree of opening of the petal limbs and the angle rotated by the anthers of the paired stamens, are shown in fig. 8, where the possession by a race of the advanced expression of either character is shown by the addition of a short line to the dot marking the position of that race. For each of the remaining eight characters the largest measurement among the racial averages of all races of both species was noted, and the racial averages were converted to percentages of this maximum measurement. The percentages of the maximum measurement were then graphed against the advancement indices of the races. The resulting graph for each character shows how that character has evolved in relation to the ten characters contributing to the advancement indices, considered as a whole. A straight line for all eight characters would indicate that they evolved simultaneously and at the same rate in relation to each other in all races. The slope of a line would indicate the magnitude of the change in relation to the absolute size of a character.

A consideration of figs. 7 to 14 shows that for six of the characters contributing to the advancement indices — namely the percentage of auto-fertilization, the maximum branch length, the number of flowers per plant, the average petal length, the average petal emargination depth and the average pistil length — the points show a reasonable agreement with a straight line. These characters have evolved gradually and at a relatively uniform rate in relation to each other in all races. But it is obvious from the varying amounts of scatter in the graphs that some characters, *e.g.*, the average number of flowers per plant, have evolved more uniformly than others such as the average petal emargination depth. Moreover, there are occasional points widely separated from all others on a graph, *e.g.*, that for race a4 (advancement index 70) in fig. 10. Such points indicate exceptions to the relatively uniform evolution of a character. The amount of change in relation to the magnitude of the character involved in the six graphs approximating straight lines varies considerably. For example, in the trend towards a decrease in the length of branches, the lowest average measurement is only 14 per cent of the highest average measurement, whereas the lowest average petal length measurement is still 62 per cent of the highest average measurement.

The graphs for the percentage of positive results on self-pollination versus the advancement index and for the pollen: ovule index versus the advancement index obviously do not follow a straight line. This reflects the fact that self-

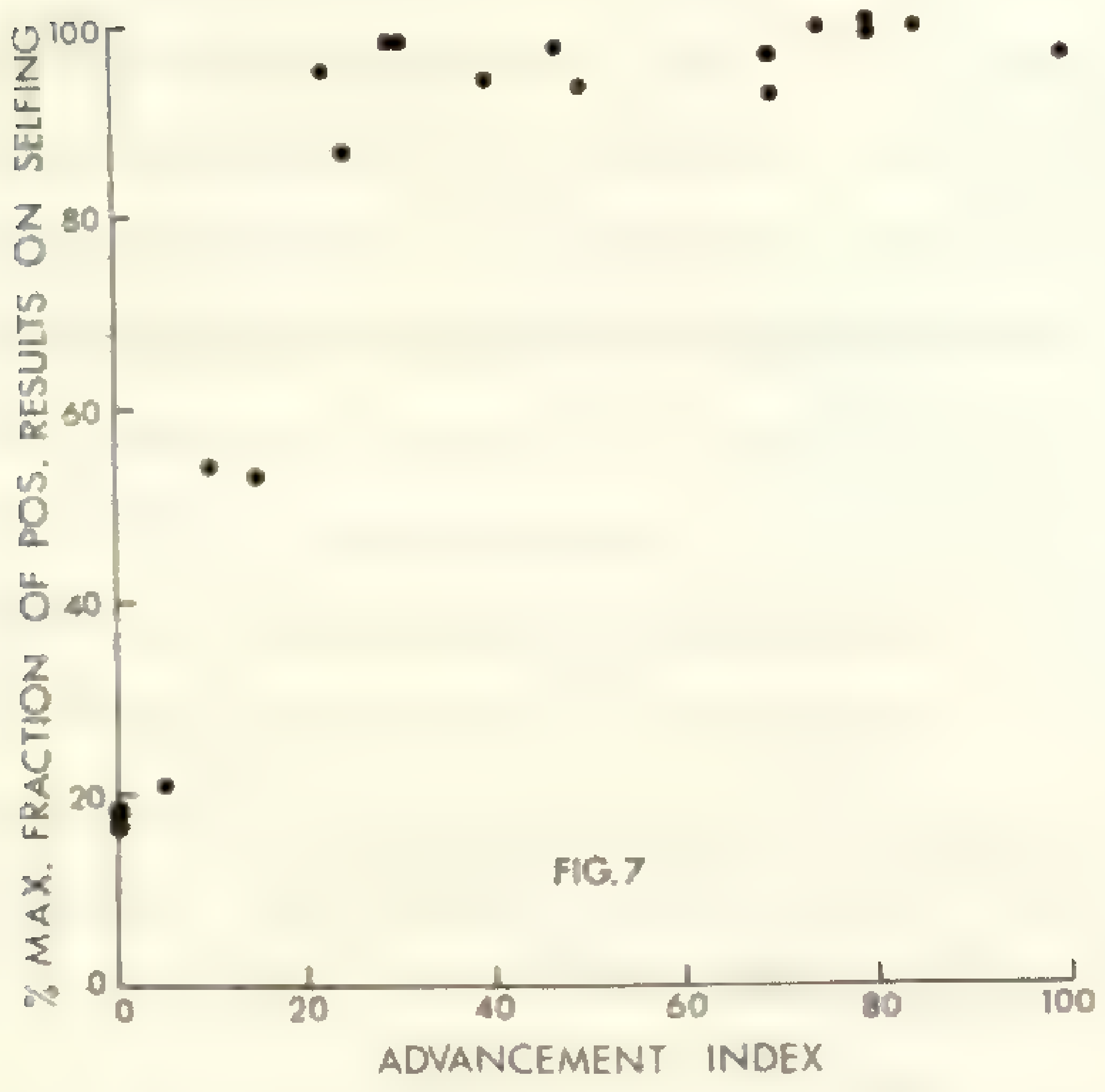


FIG. 7

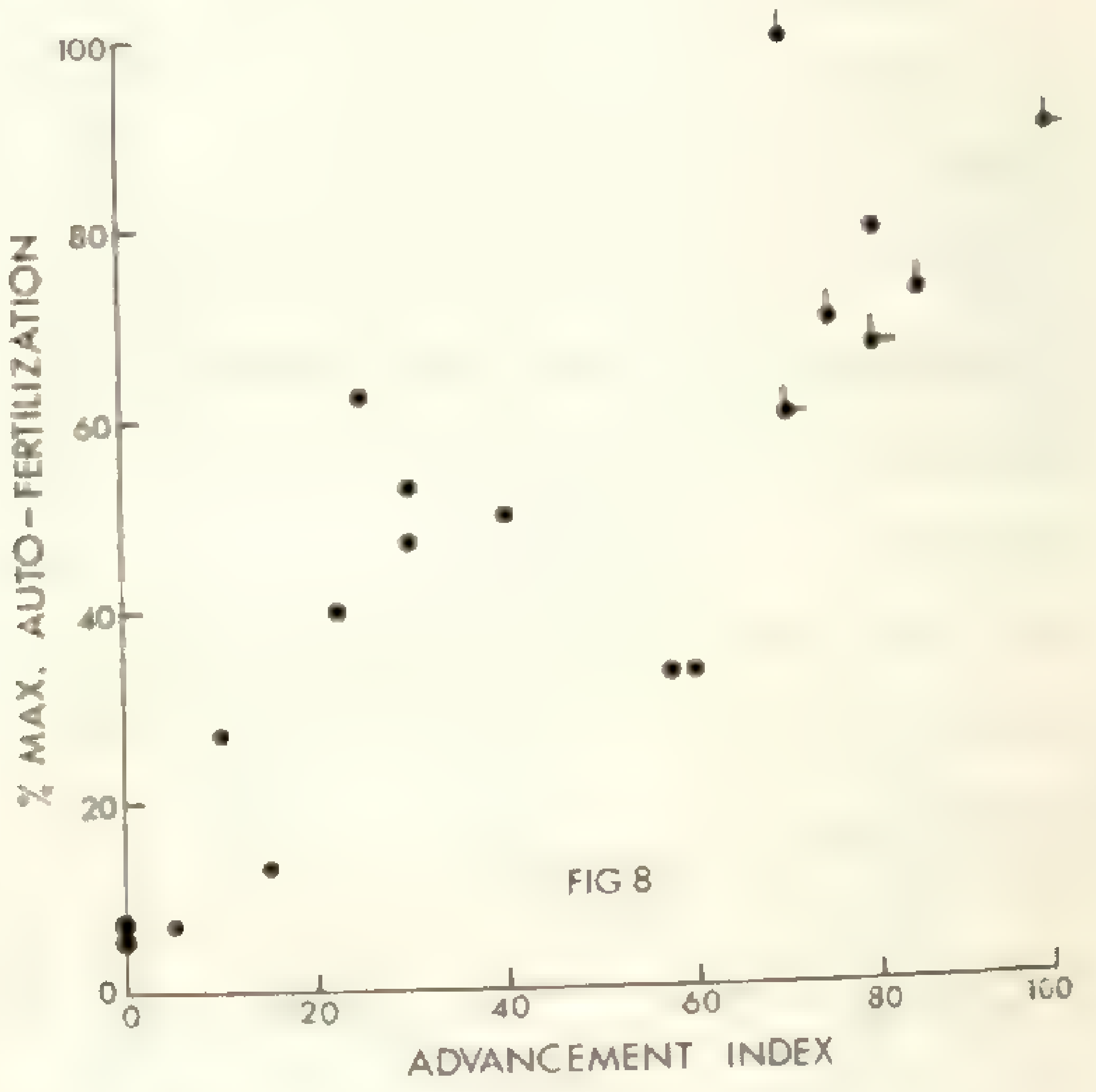


FIG 8

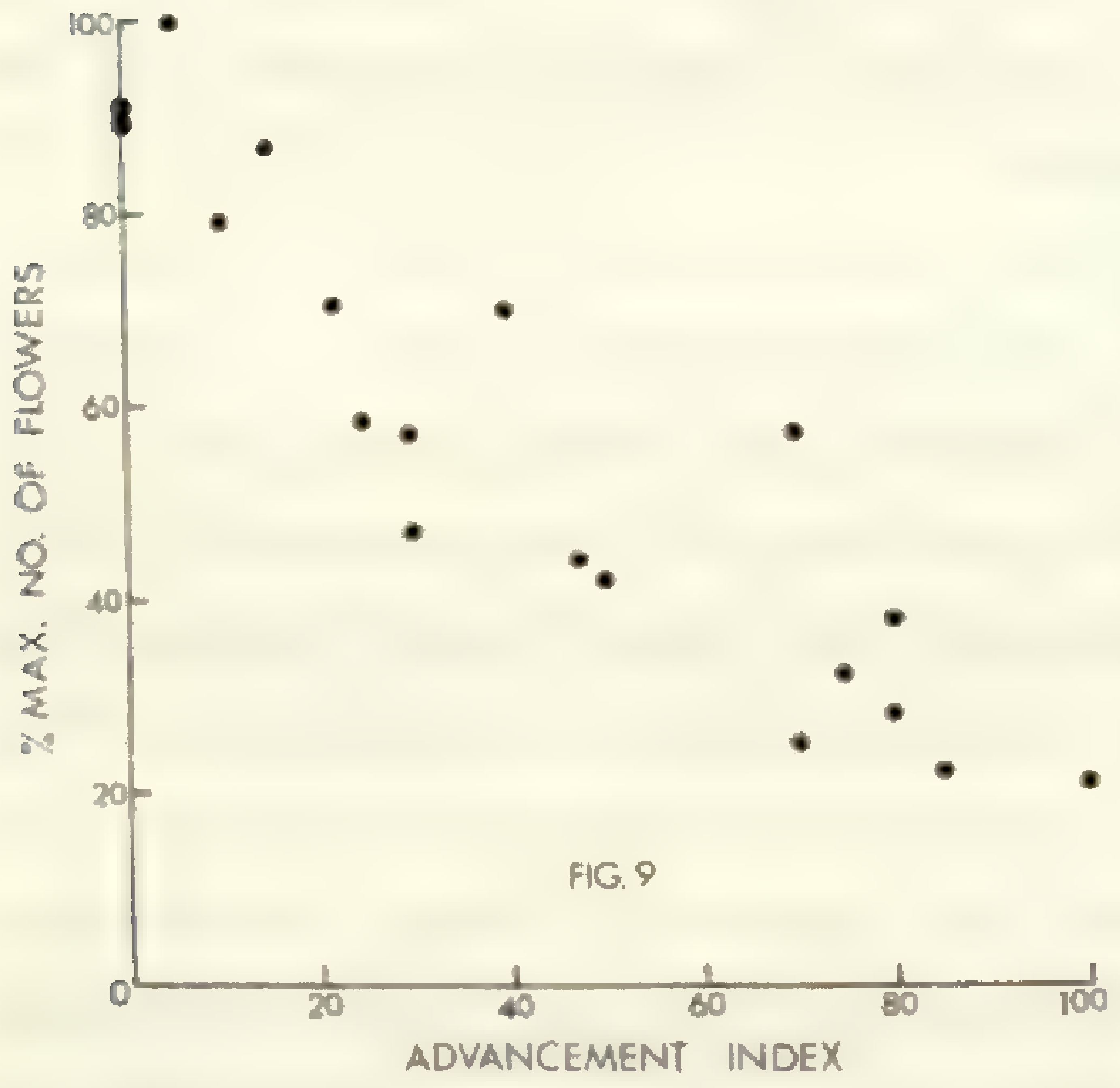


FIG. 9

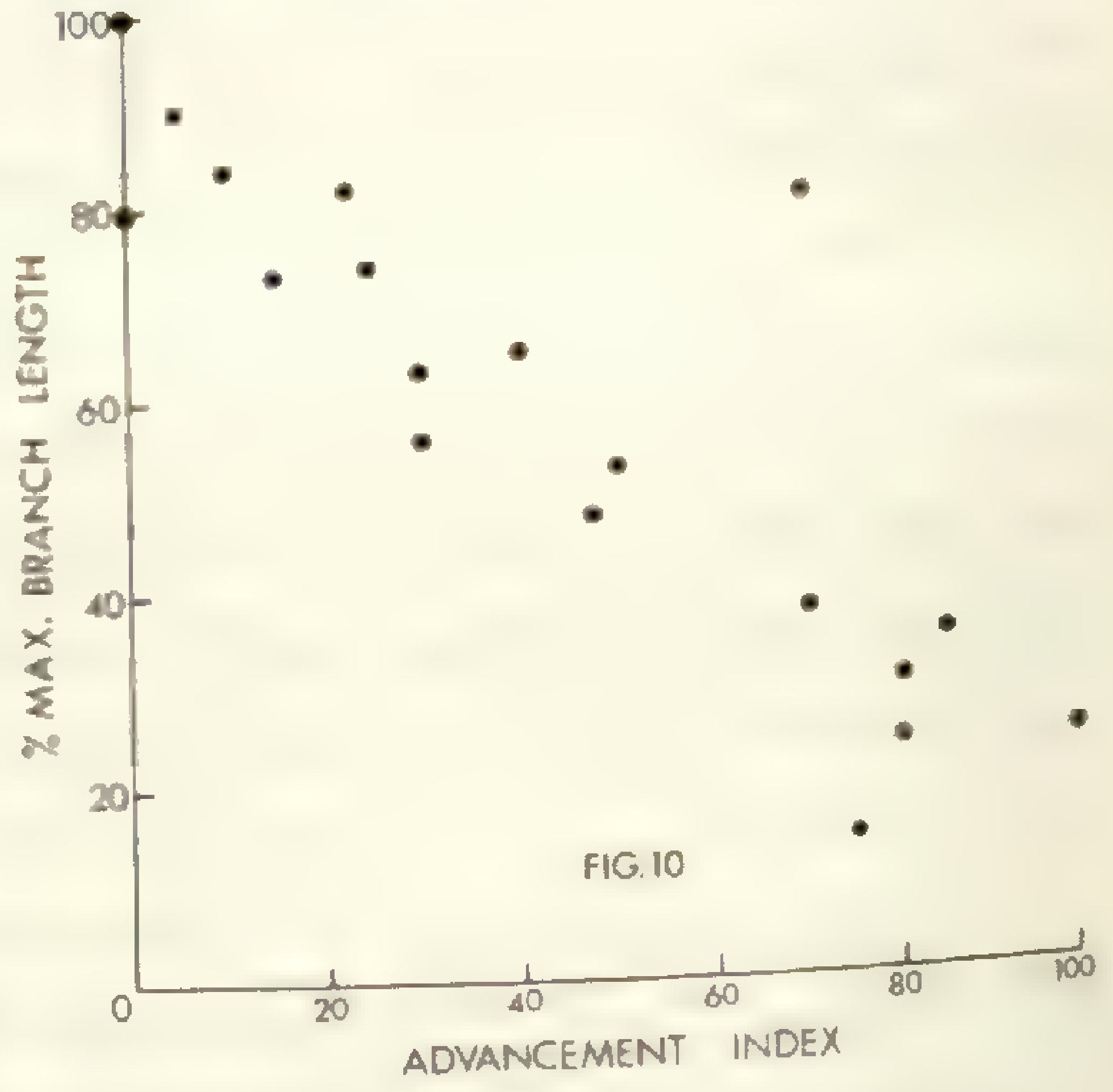


FIG. 10

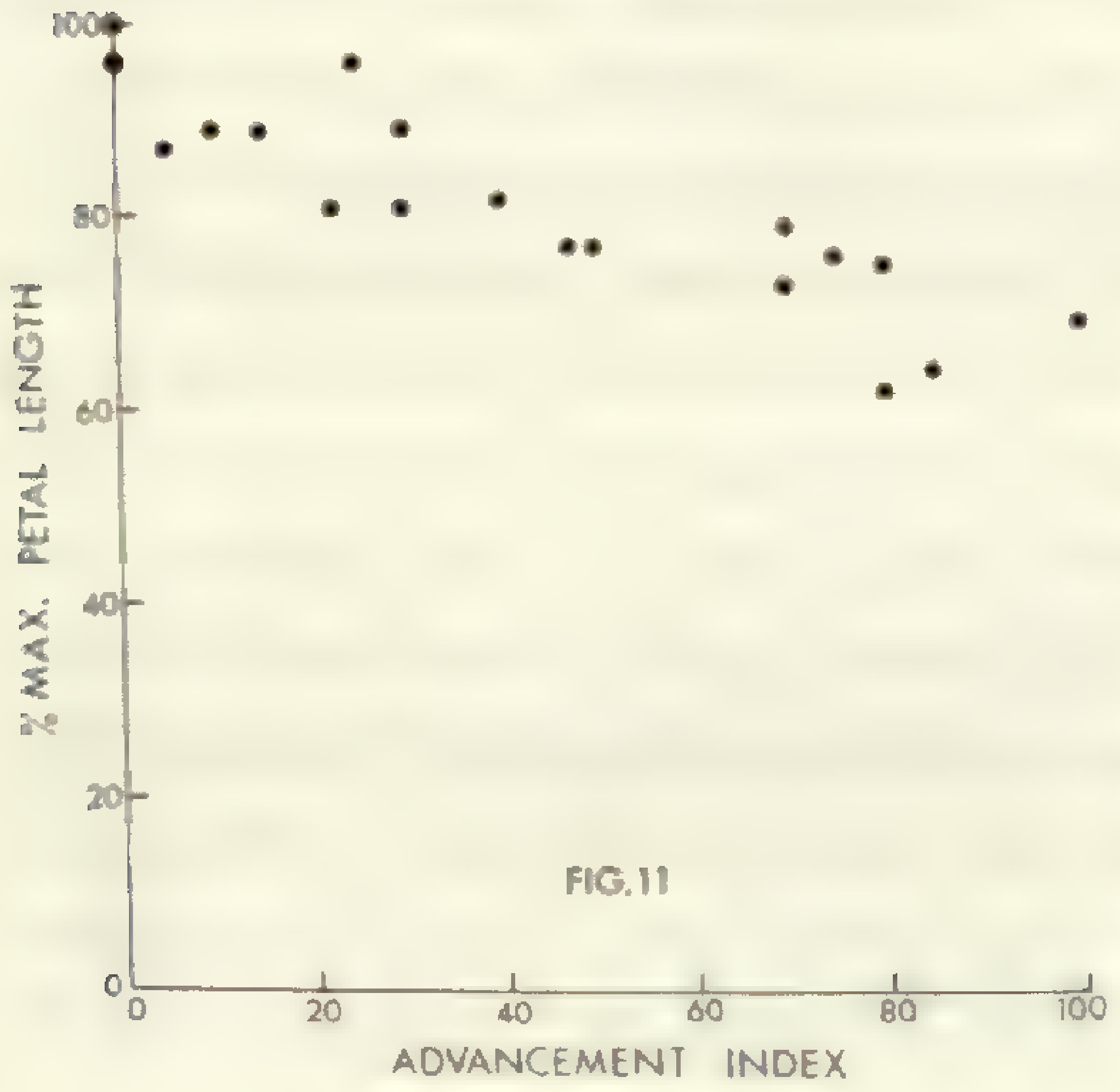


FIG. 11

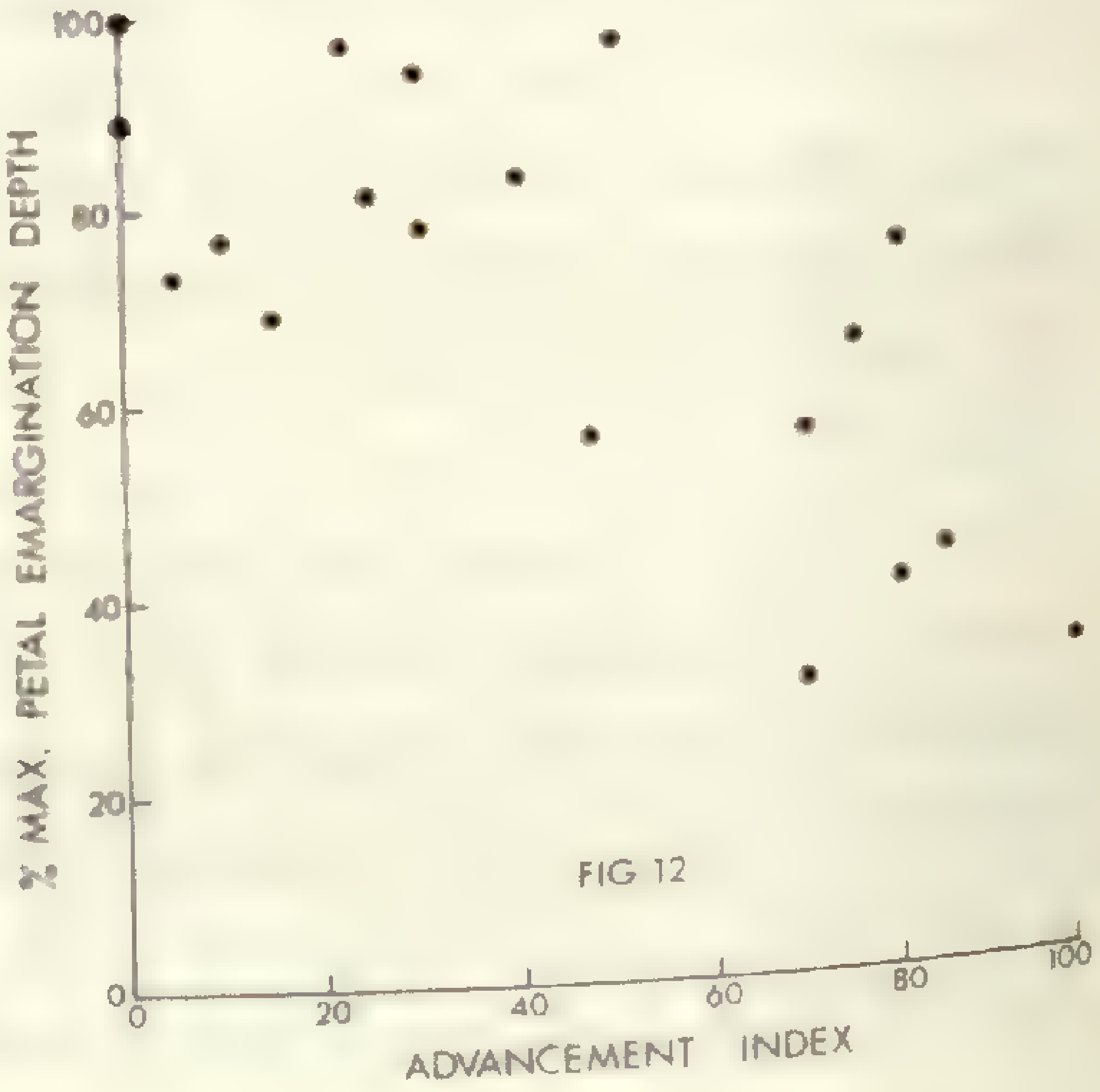
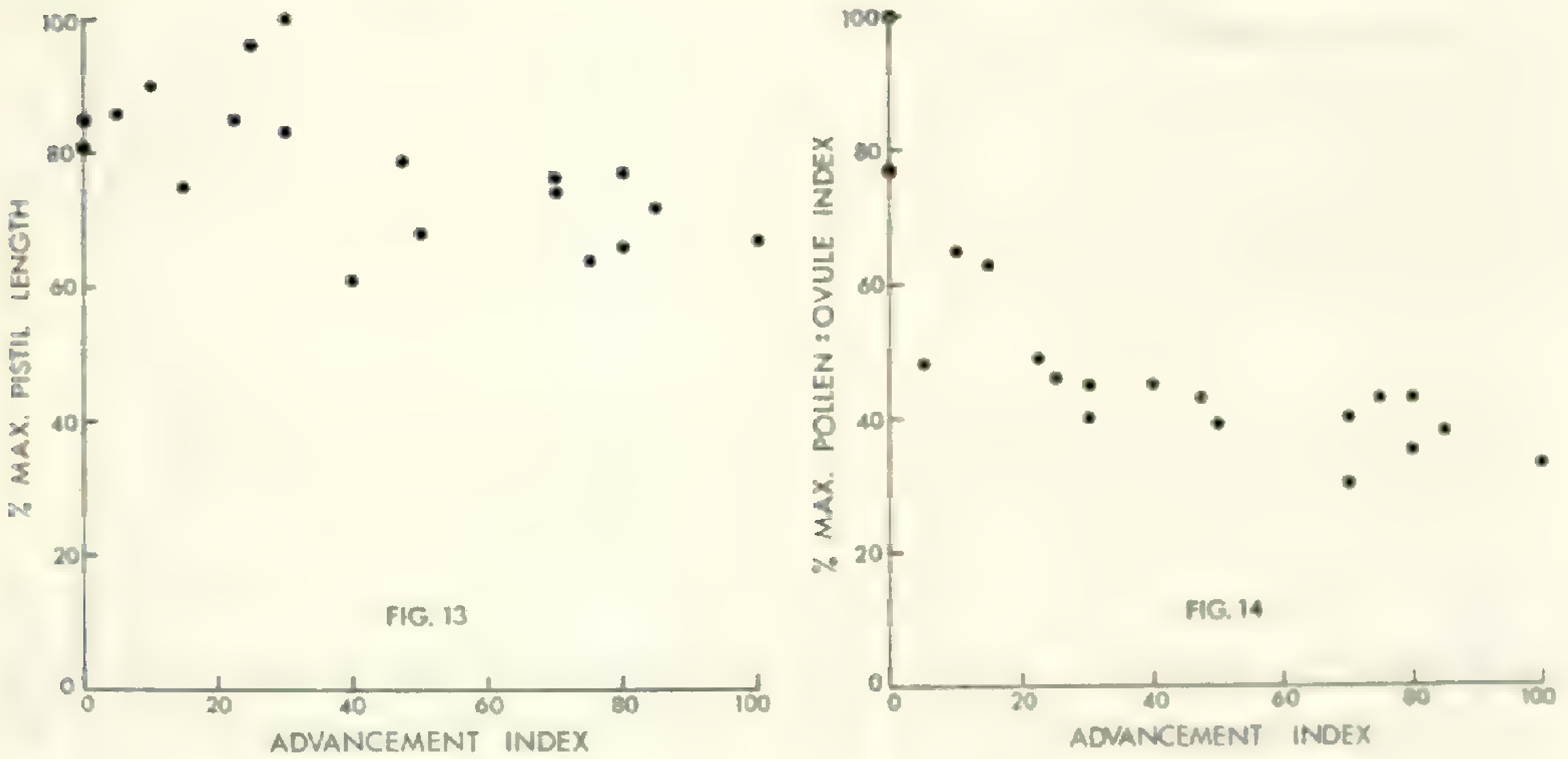


FIG 12



FIGS. 7 TO 14. Graphs of the relationships between race averages of measurements of eight characters and the advancement indices of the nineteen described races of *L. crassa*. The measurements on the ordinate are shown as percentages of the largest racial average for a character. In FIG. 8, a horizontal line attached to a point indicates a race with regularly introrse anthers, and a vertical line indicates a race in which the petal limbs bend at less than 90° to the petal claws in open flowers.

incompatibility was lost before the other characters had evolved very far, and most of the decrease in the pollen: ovule indices occurred during the loss of self-incompatibility, and there has been only a small amount of subsequent evolution of this character in the self-compatible populations.

On the other hand, the evolution of introrse anthers and of semi-erect petal limbs has occurred only in races with advancement indices of 70 or more (fig. 8), that is, only after the self-compatible populations have evolved to a considerable extent in other characters associated with the loss of self-incompatibility. And as mentioned previously, all of the races of *L. crassa* and *L. alabamica* have retained odoriferous flowers. The loss of odor seems to be one of the final stages in the evolution of *Leavenworthia* towards increasing autogamy and loss of adaptations to insect pollination, for it has occurred only in the uniformly self-compatible species of *Leavenworthia*, which are all more advanced in their reproductive systems than any of the races of *L. crassa* and *L. alabamica*.

In summary, it may be said that the evolution of self-compatibility and of all the other characters associated with it has been gradual and with few exceptions has followed a rather constant pattern. Most characters have evolved at a uniform rate in relation to each other, but the evolution of self-compatibility and the reduction in the pollen:ovule index have largely preceded other changes, and the evolution of introrse anthers, semi-erect petal limbs and particularly of non-odoriferous flowers has occurred only after the other characters have become quite advanced.

THE EVOLUTION AND RELATIONSHIPS OF THE RACES OF L. CRASSA AND L. ALABAMICA

The loss of self-incompatibility and the concomitant changes in thirteen other characters have occurred in some or all of the races of both *L. crassa* and *L. alabamica.* And at least some of these changes have occurred twice in the ancestors of other species of *Leavenworthia* (Rollins, 1963). This parallel evolution in at least four separate phyletic lines in the genus suggests the possibility that the changes have occurred more than once in either or both *L. crassa* and *L. alabamica;* so characters associated with the evolution of self-compatibility have a very limited use as indicators of relationships between the races of *L. crassa* and *L. alabamica.* Since these characters are believed to have evolved only in one direction (towards increasing autogamy and a decreasing attractiveness of the flowers to insect pollinators) they may be used instead to indicate how primitive the common ancestor of two or more races must have been. For example, as there are self-incompatible races in both *L. crassa* and *L. alabamica,* and self-incompatibility has been lost but not regained, the common ancestor of *L. crassa* and *L. alabamica* must have been self-incompatible. By similar arguments the common ancestor of *L. crassa* and *L. alabamica* was also primitive in other characters associated with the change in the breeding system.

If a phylogeny of the races of the two species could be established, it would be possible to work out from this whether characters such as self-compatibility and introrse anthers have evolved more than once in each species. Fortunately there are characters distinguishing between the races of each species which are not associated with the change in the breeding system. Some of these are shared by two or more races and may be used to indicate relationships between the races.

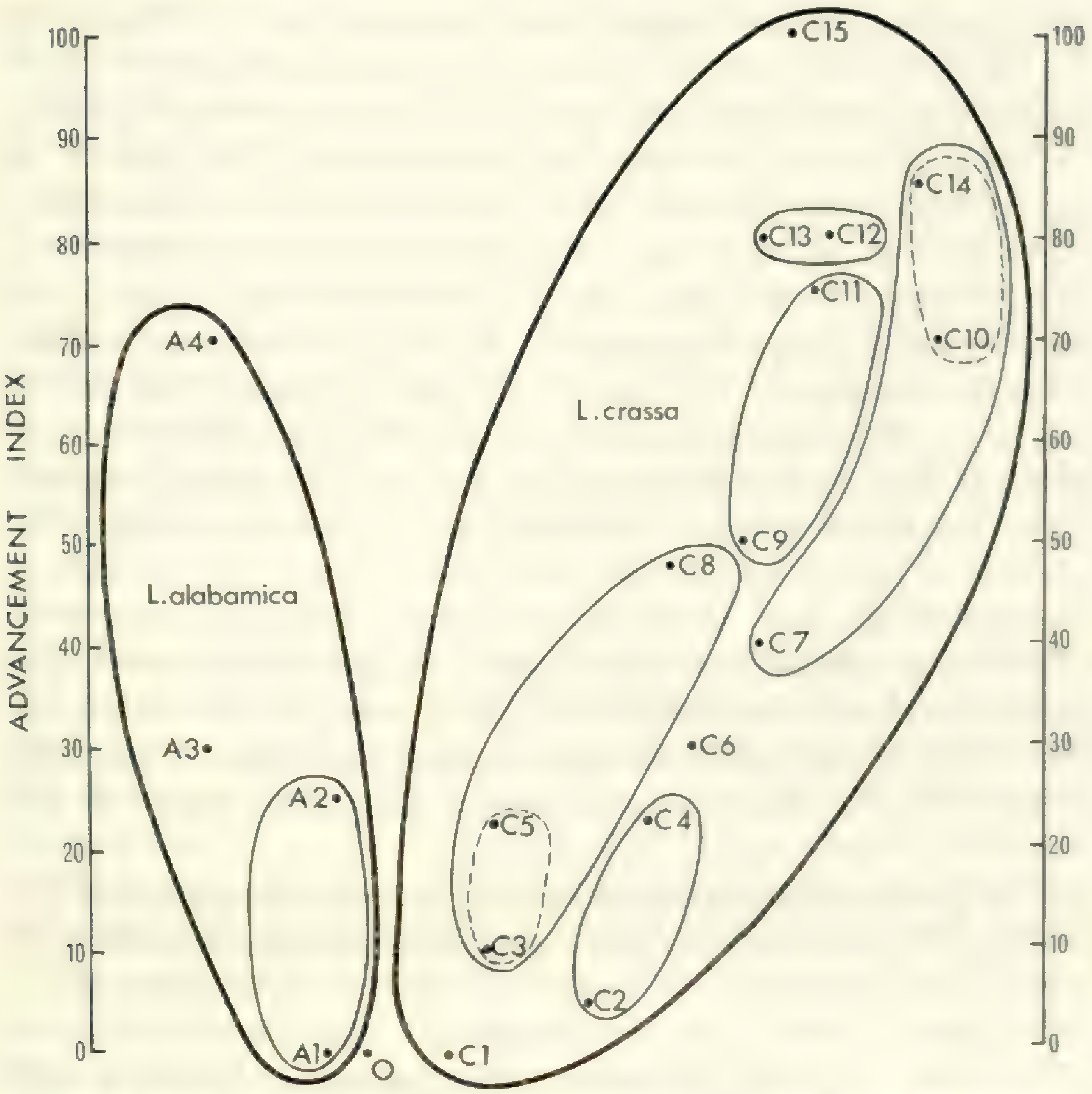


FIG. 15. Diagram of the suggested phylogeny of the races of *L. alabamica* and *L. crassa*. The point O represents the common ancestor of the two species. The advancement index (vertical axis) indicates how far a race has evolved in characters associated with the evolution of self-compatibility. The distance of each race from O on the horizontal axis represents approximately how far a race has evolved in characters not associated with the breeding system. Related races are enclosed within a curve; less inclusive curves indicate a closer relationship between enclosed races.

Moreover, the large number of races in the narrow Moulton Valley, and particularly within an area of approximately ten square miles in the Massey-Lebanon district, suggests that the races have recently diverged in this area and have migrated only short distances, so that the most closely related races may be geographically adjacent. This is apparently the case for several pairs of races, and offers valuable supporting evidence for the proposed phylogeny of the races of *L. crassa*.

The distinguishing characters and the relationships of each race have been given in the racial descriptions and only the general features of the movements and evolution of the races will be considered here. The relationships described under each race are shown in fig. 15, based on a modification of the hypothetical scheme used by Sporne (1956, fig. 7) to indicate the relationships in a group when the component taxa can be placed on an axis of increasing advancement. The position of each race on the vertical scale in fig. 15 is determined by its advancement index. The most primitive races (advancement indices=0) are at the base of the figure and the most advanced race (c15, with an advancement index of 100) is at the top of the figure. The point O represents the latest common ancestor of *L. crassa* and *L. alabamica.* The horizontal distance of a race from O shows approximately how far it has diverged from the common ancestor in characters which are not associated with the evolution of self-compatibility. The position of a race on the horizontal axis is approximate, and based on a subjective assessment of characters which vary independently of the breeding system.

The most closely related pairs of races are indicated by dotted lines around each pair. Less closely related races are shown by light solid lines around them. The races of *L. crassa* and those of *L. alabamica* are enclosed by heavier solid lines. The relationships are based on only a few characters and only those affinities which are reasonably certain have been included in fig. 15. The relationships of the more distantly related races in each species are uncertain and are not included in the diagram.

If the affinities of the races of *L. crassa* and *L. alabamica* given in fig. 15 are correct, it is apparent that many of the characters associated with the evolution of self-compatibility have evolved in parallel directions in several phyletic lines. There is no doubt that the changes have occurred independently in *L. crassa* and *L. alabamica,* and many of the quantitative and qualitative changes appear to have occurred more than once in *L. crassa* at least.

The quantitative characters vary continuously and it is highly probable that these characters have evolved gradually and repeatedly by gene changes at many loci. There is little point, therefore, in describing the extent of the quantitative changes in each phyletic line.

The loss of self-incompatibility, and the evolution of suberect petals and introrse anthers (paired stamens) can be considered qualitatively, and it is possible to decide the minimum number of times these changes have occurred in *L. crassa* and *L. alabamica.*

The loss of self-incompatibility has occurred at least once in *L. alabamica* and perhaps as many as four times, since the four self-compatible races are all geographically distant from each other. Self-compatibility has evolved three (or more?) times in *L. crassa* — in the ancestors of race c6, of races c5 and c8, and once or more in the ancestors of the remaining self-compatible races. The evolution of introrse anthers has occurred one or more times in *L. alabamica* (race a4 and the 'Russellville' and 'Tuscumbia' races) and at least twice in *L. crassa* — in races c10 and c14, in race c13, and perhaps independently also in race c15. The evolution of semi-erect petal limbs has occurred in race a4 and perhaps independently in the 'Russellville' and 'Tuscumbia' races of *L. alabamica*, and in *L. crassa* three or more times — in races c10 and c14, in race c11, in race c13 (where it is often combined with a delayed opening of the petals) and possibly independently in race c15.

Thus the evolution of self-compatibility, introrse anthers, semi-erect petal limbs and associated quantitative characters has occurred independently in several phyletic lines in *L. crassa* and *L. alabamica* (and at least twice in the ancestors of other *Leavenworthia* species — Rollins, 1963). These changes have probably been facilitated under the appropriate ecological conditions (discussed below) by the ease of self-pollination in *Leavenworthia* flowers. The anthers of the paired stamens closely surround the stigma, and the unaided transfer of pollen from the anthers to the stigma of the same flower is readily accomplished. The close proximity of the anthers and the stigma allows autogamous pollination to be effective as soon as self-compatibility has evolved; this is confirmed by the considerable auto-fertilization found under greenhouse conditions in the extrorse self-compatible races.

The self-incompatible races of *L. crassa* and *L. alabamica* may be compared with the self-compatible races with regard to the magnitude of the differences between the races, i.e. the amount of evolution that has occurred in self-incompatible and self-compatible phylads. In general, the self-compatible races are more distinct than the self-incompatible races. This applies both to characters which are associated with the change in the breeding system and to those which are not, and is reflected in the generally greater distances between self-compatible races along both the vertical and horizontal axes in fig. 15.

The self-incompatible races are more similar to each other in the characters associated with the breeding system, since the majority of these characters are adaptations to bee pollination, and apparently have been held constant in the self-incompatible races of *L. crassa* and *L. alabamica* (and in *L. stylosa*) by stabilizing selection caused by the need for cross-pollination. The self-compatible races, on the other hand, are variously adapted to a mixture of cross- and self-pollination, and there are considerable differences between the races in the characters associated with the evolution of self-compatibility. In other words, there is only one adaptive peak in *Leavenworthia* for those species and races which rely on cross-pollination, but numerous adaptive combinations of the same characters have been adopted by those races which are frequently or predominantly self-pollinated.

The greater variety of the self-compatible races in characters which are not associated with the evolution of self-compatibility is more surprising. Many of these characters are leaf characters, and it is very striking that most of the aberrant leaf characters occur in advanced races of *L. crassa* and *L. alabamica*. It may be that the more marginal habitats occupied by self-compatible races (see below) vary more than the relatively favorable sites occupied by the self-incompatible races. Morley (1959) believes that "in general the rate of evolution has been independent of population characteristics . . . and is principally a function of rates of changes in the environment." Whether or not this is the explanation for the generally greater differences between self-compatible races than between self-incompatible races, there is no evidence in *L. crassa* and *L. alabamica* that a lower genetic variability in self-compatible races has restricted their evolutionary potential.

THE COMPARATIVE DISTRIBUTIONS OF SELF-INCOMPATIBLE AND SELF-COMPATIBLE RACES

Self-compatible species are often more widespread than their self-incompatible relatives (Baker, 1953) ; this is very striking in those genera with one or more widespread self-compatible weed species. In the *Leavenworthia* species with 15 chromosome pairs, *L. stylosa*, the only self-incompatible species, has the narrowest distribution; *L. uniflora*, the species with the most advanced breeding system, is also the most widespread species of the group (and of the genus as a whole — Rollins, 1963). This suggests that the self-compatible species are better able to spread into new areas.

The distribution of the races of *L. crassa* offers a striking contrast to that of the species with 15 chromosome pairs. Not all of the glade sites are known, particularly for the self-incompatible races, but present knowledge suggests that the self-incompatible races are in general more widespread than the self-compatible races.

Except for race c3, the glade sites of the self-incompatible races of *L. crassa* are incompletely known, but the distribution of the cultivated populations of races c1, c2 and c4 suggests that there may be a number of well separated glade sites for each of these races. In addition the self-incompatible races are spread over a distance of approximately ten miles. On the other hand all of the self-compatible races of *L. crassa* are extremely local and all except race c6 occur in the Massey-Lebanon district of Morgan County where the most widely separated glades of *L. crassa* are only one and a half miles apart. Race c6 occurs approximately five miles southwest of the Massey-Lebanon district, and has probably become self-compatible independently of the Massey-Lebanon races of *L. crassa*.

The more restricted distribution of the self-compatible races of *L. crassa* is probably related to their very recent differentiation. They simply have not had sufficient time to spread very far. It is noteworthy that *the* most advanced races in both *L. crassa* and *L. alabamica* — races c15 and a4, respectively — are the most widespread races in the Massey-Lebanon district, although they have spread less than two miles. In addition, *L. uniflora* is more advanced than any race of *L. crassa* or *L. alabamica*, and is more widespread in the Massey-Lebanon district and surrounding areas than either race c15 or a4. So on a very small scale in the Massey-Lebanon district the races of *L. alabamica*, *L. crassa* and *L. uniflora* show a distribution pattern similar to that of the n=15 species; but within *L. crassa* as a whole, there is a reverse pattern, with the more primitive races being more widespread.

In *L. alabamica,* glade sites of the self-incompatible race a1 are spread over a distance of approximately 15 miles in Franklin and Lawrence counties (map 1). The glade populations of the self-compatible races a2 and the 'Tuscumbia' race occur over an almost equally large area, but the self-compatible races a3 and a4 are restricted to the smaller Massey-Lebanon district. No glade site is known for the self-compatible 'Russellville' race but the position of the only known population at the head of a narrow valley suggests that the Russellville race has the narrowest distribution of all *L. alabamica* races. The four self-compatible races of *L. alabamica* are widely separated in the Moulton and Tennessee valleys. This does not mean, however, that a common self-compatible ancestor of these four races has migrated a long distance through these valleys, as there is a strong possibility that self-compatibility has evolved several times in *L. alabamica.* There is, therefore, no clear difference between the distribution of self-incompatible and self-compatible races of *L. alabamica.*

It will be shown below that the advanced races of *L. crassa* and *L. alabamica* flower earlier than the primitive races. Within the n=15 group of species too, *L. stylosa,* the most primitive species, continues flowering the longest, and *L. uniflora,* the most advanced species, has the earliest flowering period. I believe that the earlier flowering of advanced races and species of *Leavenworthia* explains their wider distribution in the Massey-Lebanon district, and in the n=15 species. These races and species are capable of existing in more marginal habitats, and can consequently spread over areas that provide an impassable barrier to the primitive races and species.

According to this explanation, the distribution of the races of *L. crassa* is controlled primarily by historical factors, *viz.* the recent origin of self-compatible races, and the ability of advanced races to occupy marginal habitats has had little chance to influence their distribution. But in the older species with 15 chromosome pairs the relative distribution of the species is primarily controlled by their ecological tolerance, so there is an inverse relationship between primitiveness and area occupied. The situation in *L. alabamica* is intermediate between that in *L. crassa* and that in the species with 15 chromosome pairs.

THE SPREAD OF L. CRASSA AND L. ALABAMICA ONTO CULTIVATED LAND

The clearing of forest in the Moulton Valley since about 1840 has made large areas of ground near cedar glades available for occupation by *L. crassa* and *L. alabamica* populations. All of the races of *L. alabamica* and all but four of the races of *L. crassa* (races c11, c12, c13 and c14) have spread to some extent onto land from which the original forest has been cleared. Some of these races, such as c9 and c10, have spread only a very small distance from the parental glade site, but others, particularly races c2, c5, c15 and a4, have moved up to three miles over cultivated land and have produced a large number of populations growing on suitable cultivated land. On regularly cultivated land the secondary populations may contain ten or a hundred times as many plants as the glade sites from which they came, and many of the individual plants may be as large as, or larger than, the plants grown in the greenhouse.

The cedar glades are unsuitable for cultivation and have remained relatively undisturbed, except where the forest has been cleared from their borders. Consequently most if not all of those glades that originally contained *Leavenworthia* populations still do. It is therefore possible to trace the origins and movements of the populations on cultivated land with considerable certainty in most cases. This does not apply of course to those races (c1, c6, c8 and a3) for which no glade site is known.

The distribution of the field populations of the races of *L. crassa* and *L. alabamica* is shown in maps 1 to 5. The movements of the populations of each race are discussed under the description of the appropriate race above, and only the general aspects of the spread of *L. crassa* and *L. alabamica* onto cultivated ground will be dealt with here.

There is no relation between the breeding system of a race and the extent of its spread onto cultivated land. Instead the extent of the spread of each race seems to be principally determined by the accessibility of suitable land adjacent to the cedar glade populations. The most important factor in this regard is whether any of the forest surrounding a glade has been removed. Only two of the known glades still completely surrounded by forest have produced any populations on cultivated land. One of these glade populations, number 769 of race c9, has produced a single small population immediately outside the forest, directly downhill from population 769 in a drainage depression. The other glade population, number 698 of race c10, is connected to cleared land by a narrow farm road and a few seeds have apparently moved along this, perhaps on farm machinery, to form a small population in the adjacent field.

The Massey-Lebanon district is the only area where both the glade and derived field populations have been exhaustively traced. It is obvious here that almost all of the movement of populations across cultivated land has been a slow spreading of the populations over suitable land. Only two races, c15 and a4, appear to have spread through downstream dispersal of their seeds. The reason for this is that the Massey-Lebanon district is on the southern edge of the Moulton Valley, and only a few small streams run through the area occupied by *L. crassa* and *L. alabamica*. None of these originates in the low hills containing cedar glades on their slopes and at their bases. Consequently the races of *L. crassa* and *L. alabamica* in the Massey-Lebanon district have reached the streams at some distance from their source, where the streams flow between well-developed banks, below the surface of the land. At this stage in their course the streams seem to offer a barrier to the movement of *Leavenworthia* rather than an avenue for dispersal.

The other areas occupied by *Leavenworthia* are less well known; many of the known cedar glades in the Moulton Valley outside of the Lebanon-Massey district occur beside streams flowing over exposed bedrock, and it is possible that downstream transport of seeds has played a much more important role in the movement of *L. crassa* and *L. alabamica* over cultivated ground elsewhere than in the Massey-Lebanon district.

Once a population has spread onto land cleared of forest its size and subsequent migrations are controlled by the nature of the agricultural practices in the immediate vicinity. Rollins (1963) demonstrated experimentally that *L. crassa, L. alabamica* and their hybrids are unable to with-stand competition from more aggressive weeds. Corn fields are ploughed in the spring, usually after *Leavenworthia* has fruited but before most other weeds set seed; consequently *Leavenworthia* is virtually free of competition from other plants and grows most luxuriantly and abundantly in such fields. Fields which have been left uncultivated for some years have a tall but incomplete cover of weeds and *Leavenworthia* is less successful in these. Fields sown in pasture are marginal sites for *Leavenworthia*, and populations cannot survive indefinitely unless the fields are reploughed.

The precarious existence of *Leavenworthia* on grazed land was dramatically demonstrated by a population of race c15 two and a half miles south-southwest of Lebanon. In 1961 this was a small population of perhaps 50 plants in a wet depression within a pasture. The plants were mostly large and vigorous and they set abundant seed, but in 1962 and 1964 there was not a single plant, although there had been no apparent change in the farming of this field.

The *Leavenworthia* plants on regularly cultivated land (corn fields, or occasionally cotton or oat fields) are usually in the last stages of flowering when the fields dry sufficiently in the spring to be cultivated. In most years they apparently manage to produce large numbers of viable seeds, for *Leavenworthia* may cover up to several acres with one or more plants within each square foot. Even on cultivated fields, however, the number of *Leavenworthia* plants may be drastically reduced in one year if the field is ploughed earlier (or more deeply?) than usual or is left uncultivated. For example, in 1961 population 37 (race c3) covered the whole area of the corn field it occupied, and there were many large plants. In the spring of 1961 only about two-thirds of the field was ploughed (on April 23); it was one of the first fields in the area to be cultivated. The following year there were many smaller plants in the uncultivated portion, but on the cultivated portion the number of plants was perhaps only one hundredth of the number present in the previous year.

Within many cultivated fields, and in all pastures and neglected fields, *Leavenworthia* occupies only a portion of the total area, and often occurs as several separate and scattered populations. The limited distribution of the races in many suitable fields, and the small distances travelled by all of the races (never more than 3 miles in the Massey-Lebanon district at least) confirm the extremely limited powers of dispersal of *L. crassa* and *L. alabamica* noted below. The seeds have no special adaptations for dispersal, and much of the movement over the fields is probably through the movement of soil on farm equipment.

INTERSPECIFIC AND INTER-RACIAL HYBRID POPULATIONS IN THE MASSEY-LEBANON DISTRICT

The distribution pattern of the races of *L. crassa* and *L. alabamica* is even more complicated in fields which are occupied by more than one race. This occurs only in the Massey-Lebanon district, where the glade sites of thirteen races are within an area of approximately ten square miles. In each case where separate races of *L. crassa* and/or *L. alabamica* have come into contact there has been some hybridization, although none of the mixed populations is uniformly intermediate between the component races. For example, populations 276 (race a4) and 298 (race c7) are contiguous, but the bulk of the plants appear to be either pure race a4 or pure race c7, and there are only a few hybrids at the point where the races are in contact. The absence of large numbers of hybrids is probably due to the predominant inbreeding in both races and to the limited dispersal of seeds, rather than to the presence of isolating mechanisms. I have, however, done no work on the composition of the hybrid populations other than to establish their existence and identity and to plot their distribution and extent.

The maps of the distributions of the races of *L. crassa* and *L. alabamica* in the Massey-Lebanon district (maps 2 to 5) show that there are many interspecific and inter-racial hybrid populations, and sometimes several combinations are present in one field. The complexity of the racial distributions is greatest in the series of fields one and a half to one and three-quarter miles southeast of Massey where four races (c5, c7, c15 and a4) have spread onto the same fields.

The following is a brief summary of the hybrid populations occurring in the Massey-Lebanon district. The individual interspecific and inter-racial mixtures and hybrid swarms are discussed in more detail under the descriptions of the races. With one exception the mixed populations occur on secondary sites from which the forest has been removed. The single exception, described on page 94, is the small amount of admixture between the contiguous glade populations 742 (c11) and 741 (race c12?).

Adjacent populations in a series of fields with the same racial combination may be considered as due to a single contact between the races in that area. Using this simplification, there are ten distinct areas where races of *L. crassa* and/or *L. alabamica* have met and hybridized; nine of these are on cultivated sites. The numbers given here for each contact between two or more races correspond to those on the maps of the Massey-Lebanon district (maps 2 to 5).

1. Races c3 and c5 have become mixed in a complex series of corn field populations one and a half miles northeast to one and three quarter miles north-northeast of Massey.
2. Races c5 and c15 (and c7 also?) are mixed in four adjacent populations one and a half miles southeast of Massey.
3. Races c5 and a4 are mixed in the area one and a quarter to one and a half miles east of Massey.
4. A population of race c5 one and three-quarter miles southeast of Massey in 1962 contained one plant which was a hybrid between races c5 and a4. This plant is apparently a remnant of an earlier expansion of the present race a4 population farther west.
5. Races c7 and c15 are mixed in a series of populations south of glade population 361 (race c7) one and three-quarter miles southeast of Massey. There are probably minor contributions from race c5 also in the easternmost populations of the series.
6. Races c7 and a4 are mixed at the common border of contiguous populations of the two races one and a half miles south-southeast of Massey.
7. Races c11 and c12 have mixed to a small extent in the contiguous glade populations 741 (race c12?) and 742 (race c11) one and a half miles east-southeast of Massey.
8. Races c15 and a4 are mixed in a corn field two and a half miles south-southwest of Lebanon.
9. Races c15 and a4 are also mixed in scattered populations one and a quarter miles south-southwest to three-quarters of a mile east of Lebanon.
10. Races a3, a4 and c15 are mixed in portions of the only known population of race a3, two and three-quarter miles south-southeast of Massey.

Ignoring the possibility that race c7 may occur in area 2 above and that race c5 may occur in area 5, the ten areas represent eight different racial combinations within an area of approximately ten square miles. Two combinations (races c5 and a4, races c15 and a4) have occurred twice in widely separated areas.

Four races of *L. crassa* (c3, c5, c7 and c15) and two (a3 and a4) of *L. alabamica* contribute to the mixed populations on secondary sites; two other races of *L. crassa* (c11 and c12?) have mixed slightly at one glade site. With regard to the species involved, four of the contacts (including the one on the glade site) involve two races of *L. crassa,* five involve one race of *L. crassa* and one race of *L. alabamica,* and one involves two races of *L. alabamica* and one race of *L. crassa.*

Races c5, c15 and a4 have come into contact most often with other races. These three races are also the ones which have spread most widely over the fields; their larger number of contacts is due to their greater spread.

There are several areas where separate races of *L. crassa* and/or *L. alabamica* occur on different sections of the same field, or in adjacent fields, but have not yet met and hybridized. If future agricultural practices permit the spread of these populations, additional racial mixtures will undoubtedly occur.

THE GLADE POPULATIONS OF L. CRASSA AND L. ALABAMICA

Leavenworthia alabamica and *L. crassa* are endemic to northwest Alabama. They occur naturally on cedar glades — small isolated areas where the horizontally-bedded limestone develops shallow, denuded soils unable to support forest. The limestone outcrops in northwest Alabama occur in two parallel valley systems — the Tennessee Valley proper and the Moulton Valley (map 1). The Tennessee Valley contains only a few populations of *L. alabamica,* in Colbert County, on Bangor or Tuscumbia limestones of Mississippian age.

The Moulton Valley is a narrow valley approximately fifty miles long in an east-west direction, and three to ten miles wide (Johnston, 1930). The floor of the valley consists entirely of Bangor limestone of Mississippian age, except at the western end, where the limestone is overlain in parts by a thin veneer of coastal plain deposits of the Tuscaloosa (Cretaceous) formation. To the north, the Moulton Valley is separated from the Tennessee Valley by Little Mountain, a low lying sandstone plateau 100 to 250 feet high. The Moulton Valley is bounded on the south by the Pottsville escarpment, which rises 200 to 500 feet above the Moulton Valley to the Sand Mountain Plateau, an extension of the Cumberland Plateau. Most of the Bangor limestone of the Moulton Valley is covered by a thin layer, up to 25 feet deep, of regolith (material overlying solid rock). The cedar glades are scattered throughout the Moulton Valley in places where the topography and the character of the underlying rock have caused denuded limestone outcrops to be exposed.

The Moulton Valley was searched for cedar glades containing *Leavenworthia* as extensively as was possible in three field seasons. The number of known glade populations of each race varies from more than ten (race a1) to zero (races c1, c6, c8, and a3). The number of undiscovered glade sites is difficult to estimate, but there are probably few in the Massey-Lebanon district, which has been intensively searched. Four races of *L. crassa* (races c1, c2, c4 and c6) and two races of *L. alabamica* (a1 and a2) occur outside of the Massey-Lebanon district, and all of these probably have undiscovered glade populations. Race c6 is known only from one cultivated site, and may well have only a single glade population. The other races outside the Massey-Lebanon district are each known from many glade or cultivated sites, and they may all have several glade populations.

In the Massey-Lebanon district there are 25 known glade sites (counting the adjacent clearings of population 743 as one glade, and the contiguous areas occupied by populations 741 and 742 as two glades) shared by eleven races of *L. crassa* and *L. alabamica* (maps 2 to 5). I would have considered that all the glades in the Massey-Lebanon district are known but for the fact that two races (c8 and a3) in the area are each known from a single cultivated population. These two cultivated populations must have come from glade sites originally, although intensive searches of the adjacent areas have failed to reveal any glade populations of races c8 and a3. It is possible that these two races have migrated a considerable distance from their glade source, but it is still surprising that an existing glade could have been overlooked. Another possibility is that the original glade sites have had the surrounding forest removed, and have become too dry to support *Leavenworthia* populations.

Assuming that there is (or was?) one glade site for race c8 and one for race c3, there are 27 glades occupied by thirteen recognized races in the Massey-Lebanon district; that is, an average of 2.1 glade populations per race. Some of the glade populations that have not been grown in the greenhouse may represent distinct races, so the average number of glades per race may be less than two. On the other hand, several populations occupy rocky outcrops that I do not consider to be pre-agricultural glade sites, but since these sites have had the surrounding forest removed, it is impossible to be certain whether or not they are secondary sites.

The Massey-Lebanon district is only 4.5 miles long and 4 miles wide, so there are a large number of allopatric races in an extremely small area. Actually, all of the glade sites for the ten races of *L. crassa* in the Massey-Lebanon district for which glade populations are known occur in an area approximately 3 miles long by half a mile wide.

THE LIMITED DISPERSAL CAPACITY OF LEAVENWORTHIA

The existence in the Massey-Lebanon district of distinct races separated by such small distances, or even in the case of populations 741 and 742 of distinguishable populations in contact at their margins, demands that both pollen and seed dispersal must be extremely restricted.

Nothing is known of the distances that non-social bees, the natural pollinators of *Leavenworthia*, fly, but there must be very few flights from one glade to another. Some species at least prefer to forage close to their nests (Linsley, 1958). Both honeybee and bumblebee (*Bombus* species) individuals characteristically forage in very small areas, sometimes for days at a time, even when suitable plants are available over a wide area (Butler, 1954; Free and Butler, 1959). The fact that the ratio of native bees to honeybees is much lower in field populations than in glade populations (see below), even where field populations are adjacent to glade populations, suggests that the native bees do not habitually travel far. The self-compatibility of many populations probably also restricts the amount of outcrossing and therefore of hybridization between races (Rollins, 1963).

Leavenworthia seeds lack adaptations for either wind or animal dispersal. Most seed movement probably occurs after heavy rains, when some of the glade soil is carried away by the flow of water over the shallow glade soils. The glades in the Massey-Lebanon district are small, however, and have no streams running through them so the seeds cannot be carried far by water movements. The movements of the *Leavenworthia* populations in the cedar glades must have been primarily controlled by the rate at which erosion exposed suitable ecological territory contiguous with that already occupied. Most of the known glades of *L. crassa* and *L. alabamica* outside of the Massey-Lebanon district have streams running through them, and it is probable that there seeds are carried downstream and establish populations at considerable distances from the parent source. It may be significant that outside of the Massey-Lebanon district the races of *L. crassa* and *L. alabamica* are much farther apart than they are within the Massey-Lebanon district.

That small distances can be effective geographical barriers is shown dramatically by several instances in the Massey-Lebanon district where two glades are less than one hundred meters apart, but contain different races. For example, populations 698 (race c10) and 699 (race c14) are quite distinct when grown in the greenhouse, although the margins of these two populations are only about twenty-five meters apart. If there has been any gene flow between these two populations, it has not occurred with sufficient frequency to cause them to become alike.

The coexistence of populations 742 (race c11), with yellow-centered flowers, and 741 (race c12?), with yellow flowers, in one glade is even more remarkable. The glade is a narrow area approximately 66 meters long and nowhere more than 4 meters wide. The southeastern section of the glade (occupied by population 742) is approximately 37 meters long, and in 1962 contained 221 plants with yellow-centered flowers, eight yellow-flowered plants, and six plants with imperfect-centered flowers (probably interracial hybrids). In this section, all of the plants with yellow flowers and imperfect-centered flowers were within one meter of the northwestern section of the glade occupied by population 741. The area occupied by population 741 in 1962 was about twenty-nine meters long and contained 218 yellow-flowered plants, 20 plants with yellow-centered flowers and 11 plants with imperfect-centered flowers. Most of the 31 non-yellow-flowered plants were close to the common margin of the two populations.

Thus these two sections of the glade are occupied by contiguous, but morphologically distinct, populations. The plants of the two populations are quite continuous, and there is no break or even a decrease in the number of plants at the junction of the two populations.

At both ends of the area occupied by these two races the stratum on which they occur continues around the hillside, but elsewhere the outcrop is at present less well developed and not occupied by *Leavenworthia.* Presumably these two races were formerly growing separately on different sections of the outcrop. As the outcrop has eroded, the flat areas suitable for *Leavenworthia* have moved together until recently they have become continuous. These movements must have been slow, and yet the amount of mixture of the races is still very small.

There are several glades in the Massey-Lebanon district which are entirely unoccupied by *Leavenworthia,* although they appear to be quite suitable and are occupied by other glade plants, and are only short distances from glades containing *Leavenworthia.* These glades are marked with a cross in map 2. In addition, there are only three glades which are occupied by both *L. crassa* and *L. uniflora,* and no glades which are occupied by *L. alabamica* and *L. uniflora. L. uniflora* is reproductively isolated from both *L. crassa* and *L. alabamica,* and coexists with both species in many cultivated sites. Moreover, in Tennessee *L. uniflora* may occur in cedar glades together with up to three other species of *Leavenworthia.* The rarity of glades with both *L. uniflora* and *L. crassa* or *L. alabamica* must be attributed to the poor ability of these species to migrate over anything but continuously suitable ground. Apparently, in the migrations of the *Leavenworthia* species in the Massey-Lebanon district very few glades have become accessible to both *L. uniflora* and *L. crassa* or *L. alabamica.*

It might be argued that differences between narrowly separated or contiguous glade populations are maintained in spite of considerable gene flow between the populations, by ecotypic adaptation to the particular soil conditions in each glade. Several factors suggest, however, that this is not the case. First, few of the characters separating races are of a sort which can be readily thought of as reflecting edaphic adaptations. Second, in the most extreme cases, where the distances between populations are least, the distinguishable populations occur on the same stratum of the same geological formation where appreciable soil differences are least likely. Third, exactly comparable situations are equally common in the recent, radically different environment of cultivated fields, where adaptive differences parallelling those in the glades are unlikely; these situations can be much more readily explained in terms of a limited dispersal capacity and population movements in response to changing farm practices.

The distribution of the species and races on cultivated ground in the Massey-Lebanon district indicates that the species have a very restricted dispersal capacity. Even if a field is totally suitable for *Leavenworthia* at present, it may be occupied by separate populations which have not been able to spread over the whole field and come into contact. This demonstrates that *Leavenworthia* pollen and seeds disperse very short distances even when there is no ecological barrier to their movement.

A COMPARISON OF SELF-INCOMPATIBLE AND SELF-COMPATIBLE GLADE POPULATIONS

The extremely limited dispersal powers of *Leavenworthia* have caused each glade population to be effectively isolated from all others. The lack of gene flow between populations has allowed many of the populations to diverge until they are now distinguishable under uniform conditions. Within the Massey-Lebanon area particularly, there are many distinct but closely related races in a very small area. These races must have evolved very close to the sites they presently occupy, and probably under conditions very similar to those existing at present.

Most of the differences between the races are associated with the evolution of self-compatibility, and therefore the races of *L. crassa* and *L. alabamica* offer an exceptional opportunity to study the selective factors which may have been responsible for the evolution of self-compatibility and the concomitant changes in other characters. A detailed study was made of the plants and the pollinators in natural glade populations of *L. crassa* and *L. alabamica* in the hope of revealing differences between the populations of self-incompatible and self-compatible races.

The cedar glade populations are all relatively small (usually with less than 1000 plants). In those glades containing less than 1500 plants, the number of plants in each glade known in 1962 was counted at the height of the flowering season with a mechanical hand-counter. The numbers obtained (table 10) are probably slight underestimates, since plants that had produced no flowers by this time could be overlooked, and occasionally two plants growing closely together might be counted as one. For the few glade populations with more than 1500 plants, the counts are estimates made by counting over the population ten plants at a time. These counts are probably correct to within less than five per cent.

There were more than 500 plants in ten of the twelve glade populations of self-incompatible races of *L. crassa* and *L. alabamica* (races c1 to c4 and a1). The two self-incompatible glade populations with less than 500 plants in 1962 (populations 743d and 66) are very close to other glade populations of the same race. The number of plants in the glade populations of self-compatible races is strikingly different; only two of the twenty glades had more than 500 plants, and the greatest number was 710 in population 745.

A number of the glades have had some or all of the forest removed from their margin and are considerably disturbed as a consequence (see table 10). The counts on these populations may not reflect the pre-agricultural size very accurately. The remaining glades (eight of self-incompatible races, fifteen of self-compatible races) have been disturbed very little or not at all by agricultural practices, and the figures given should be fair estimates of the pre-agricultural size of the populations.

The geometric mean of the number of plants in the eight self-incompatible populations in undisturbed glades was 1884 in 1962; the geometric mean of the number of plants in the fifteen self-compatible populations in undisturbed glades was 278. That is, on the average there were more than six times as many plants in the self-incompatible populations than in the self-compatible populations.

If only the 23 undisturbed glade populations are considered, the populations of self-incompatible and self-compatible races may be statistically compared. For this purpose the distribution of the number of plants per population is obviously highly skewed. The distribution was made approximately normal by taking the logarithm to the base ten of the number of plants. The logarithms of the number of plants per population in the self-incompatible and self-compatible populations were significantly different ($P<.001$) by a two-tailed 'Student's t' test, *i.e.*, the known glades of self-incompatible races contained significantly more plants in 1962 than the glades of self-compatible races.

To obtain measurements of the number of flowers produced by the plants in glade populations, a sample of plants was collected from each population at the end of the 1962 flowering season, and the number of buds and flowers (very few) and fruits was counted. I was unable to devise any practicable random or systematic sampling technique that would satisfactorily measure the average number of flowers produced by the plants in each glade. Any such technique would have to take into account the fact that the plants are very irregularly distributed in each glade. *Leavenworthia* plants usually occupy only a portion of each glade, and are concentrated in the most favorable parts of the glade, where they may be several times larger than elsewhere. Instead, a block sample from the portion of each population where the plants were densest and largest was taken. Fifty plants, comprising all the plants in a small area, were dug up and the number of buds, flowers and fruits was counted. (In the smallest populations only twenty-five plants were sampled). Since the counts were made at the end of the flowering season, the average number of flowers per plant in each sample may be taken as the average number produced by the plants of the sample during the flowering season. The average number of flowers per plant in a population is taken as half the average number of flowers per plant in the sample. This method is quite approximate and probably underestimates the average number of flowers per plant in most populations.

The estimated average number of flowers per plant in each of the undisturbed glades in 1962 is shown in table 10. The average of the estimates for the eight undisturbed self-incompatible populations is 4.92 flowers per plant, and

TABLE 10. PLANT AND FLOWER COUNTS OF GLADE POPULATIONS OF L. CRASSA AND L. ALABAMICA IN 1962

Species and Race	Selfing Status[1]	Population	No. of plants	Log$_{10}$ of no. of plants	No. of flowers per plant[2]	Estimated av. no. flowers per plant	Est. no. of flowers produced by population	Log$_{10}$ est. no. of flowers produced	Sample of plants counted on April 25		
									No. plants counted	No. plants flowering	% plants flowering
L. crassa											
Race: c1	-		No glade site is known								
c2	-		No glade site is known								
c3	-	89[3]	ca. 5,000	—	—	—	—	—	—	—	—
		61[3]	ca. 1,500	—	—	—	—	—	—	—	—
		743b	2,280	3.36	15.72	7.86	17,921	4.25	157	92	58.6
		743c	1,330	—	—	—	—	—	—	—	—
		743a	908	2.96	15.65	7.83	7,105	3.85	163	34	20.9
		743e	576	2.76	5.97	2.99	1,719	3.24	169	25	14.8
		743d	435	2.64	6.58	3.29	1,431	3.16	159	23	14.5
Race: c4	-	38	1,360	3.13	7.34	3.67	4,991	3.70	116	100	86.2
		66[3]	305	—	—	—	—	—	—	—	—
c5	+	791	451	2.65	3.81	1.91	859	2.93	158	15	9.5
		86	641	2.81	9.20	4.60	2,949	3.47	150	1	0.7
		118a	419	2.62	10.66	5.33	2,233	3.35	143	19	13.3
		118b[3]	117	—	—	—	—	—	—	—	—
c6	+		No glade site is known								
c7	+	361[3]	ca. 450	—	—	—	—	—	—	—	—
c8	+		No glade site is known								
c9	+	769	295	2.47	11.72	5.86	1,729	3.24	No flowers		0.0
c10	+	698	127	2.10	3.35	1.68	213	2.33	127	22	17.3
c11	+	742	251	2.40	9.80	4.90	1,230	3.09	124	6	4.8

c12	+	739	306	2.49	7.31	3.66	1,118	3.05	No flowers		0.0
		741	234	2.37	5.14	2.57	601	2.78	119	8	6.7
c13	+	745	710	2.85	5.28	2.64	1,874	3.27	114	4	3.5
		746	207	—	—	—	—	—	119	2	1.7
c14	+	699	215	2.33	2.04	1.02	219	2.34	145	15	10.3
c15	+	53	282	2.45	5.76	2.88	812	2.91	162	8	4.9
		27^3	ca. 200	—	—	—	—	—	—	—	—
		750^3	66	—	—	—	—	—	—	—	—
L. alabamica:											
Race: a1	–	31	ca. 5,000	3.71	10.34	5.17	25,850	4.41	111	100	90.1
		82	ca. 20,000	4.30	9.90	4.95	99,020	5.00	132	100	75.8
		922	ca. 2,000	3.30	6.88	3.44	6,880	3.84	198	78	39.4
a2	+		No glade site is known								
a3	+		No glade site is known								
a4	+	288	ca. 400	2.60	4.15	2.08	832	2.92	170	10	5.9
		60^3	?	—	—	—	—	—	—	—	—
		681	102	2.01	4.62	2.31	236	2.37	No flowers		0.0
		445	155	2.19	3.42	1.71	265	2.42	No flowers		0.0
		684	145	2.16	4.53	2.27	329	2.52	No flowers		0.0
		685^3	ca. 500	—	—	—	—	—	—	—	—

[1] – = self-incompatible, + = self-compatible.

[2] The counts of the number of flowers per plant were made in the area of each population where the plants were growing most vigorously. The estimated average number of flowers per plant is half the average number in the sample.

[3] These populations are considerably disturbed, and the number of plants in them may not closely resemble the pre-agricultural size of the populations.

the average of the estimates for the fifteen undisturbed self-compatible populations is 3.03 flowers per plant. That is, on the average, plants in the self-compatible populations produced approximately three-fifths as many flowers in 1962 as the plants in the self-incompatible populations. The difference is significant ($P<.001$) by a two-tailed 'Student's *t*' test.

So far it has been shown that self-incompatible populations of *L. crassa* and *L. alabamica* contained more plants with more flowers per plant than the self-compatible populations. The two parameters are significantly correlated in the 23 undisturbed populations ($r=.54$, $P<.01$). This is shown graphically in fig. 16, where the estimates of the number flowers per plant are plotted against the logarithm of the number of plants in each glade population. The self-incompatible populations are concentrated in the upper right section of the graph, and the self-compatible populations in the lower left section.

The number of plants in a population multiplied by the estimated number of flowers per plant in the same population gives an estimate of the number of flowers produced in 1962 in each undisturbed glade (table 10). As expected there is a considerable difference between self-incompatible and self-compatible populations in the number of flowers produced in each glade. All but two of the eight self-incompatible populations produced more than 2000 flowers in 1962, and all but two of the fifteen self-compatible populations produced less than 2000 flowers. The geometric mean of the number of flowers produced in the 1962 flowering season in the eight self-incompatible populations was 8,650; the geometric mean of the number of flowers produced in the fifteen self-compatible populations was 736. The difference between self-incompatible and self-compatible populations was again significant ($P<.001$) by a two-tailed 'Student's *t*' test; this is to be expected, since the two contributing parameters, the number of plants per population and the estimated average number of flowers per plant, were both significantly different in self-incompatible and self-compatible populations.

It is apparent that the self-compatible populations occupy poorer glade sites than the self-incompatible populations. In the poorest glades, such as those of population 698 (race

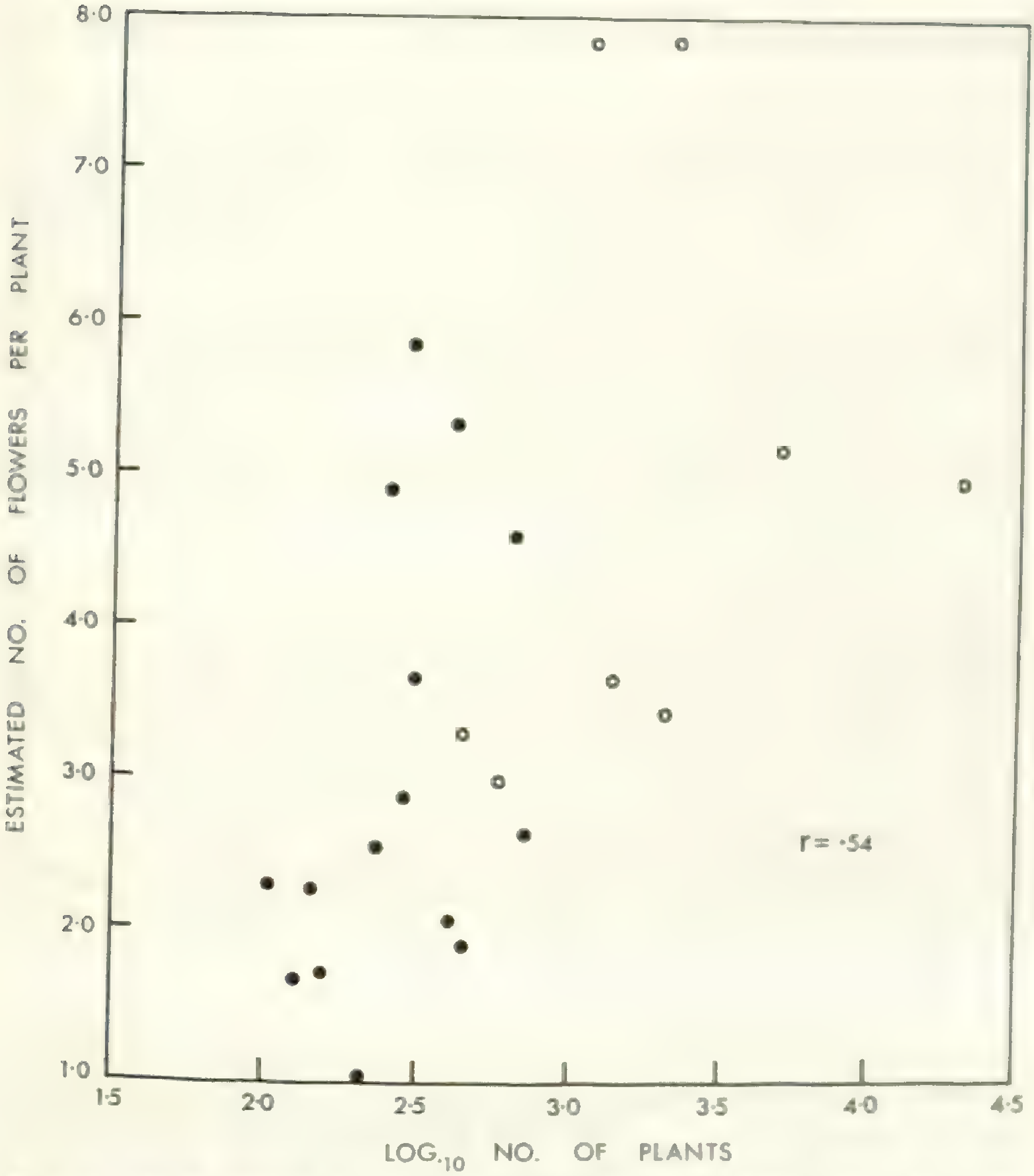


FIG. 16. The relationship between the number of plants and the estimated average number of flowers per plant in undisturbed glade populations of *L. crassa* and *L. alabamica* in 1962. Open circles represent self-incompatible populations; closed circles represent self-compatible populations.

c10) and 699 (race c14), it is estimated that there are less than two flowers per plant on the average (table 10). Under poor conditions there are also fewer seeds per silique — perhaps an average of two seeds per silique. These populations clearly live under very marginal conditions.

Leavenworthia species are amongst the most hydrophilic of cedar glade plants (Freeman, 1933). The principal factor limiting the distribution and growth of *Leavenworthia* is the availability of soil water in the spring (Quarterman, 1950; Rollins, 1963); the production of flowers and the growth of seeds are severely curtailed by the drying of the glades in the spring as the temperature increases and the rainfall decreases.

If the small number of plants and of flowers per plant in the self-compatible populations is due to the populations being on drier sites, it would be expected that these populations would stop flowering earlier than those of self-incompatible races. This was investigated by counting the percentage of plants that were still producing flowers late in the flowering season (April 25, 1962) in a sample from the most favorable portion of each glade. The results (table 10) show that, in general, there is a much higher percentage of plants still flowering in the self-incompatible populations than in the self-compatible populations. In fact, the distinction between self-incompatible and self-compatible populations is clearer in these figures than in the figures for the number of plants per population and the estimated average number of flowers per plant. Only one self-compatible population (698, race c10) had a higher percentage of plants flowering on April 25, 1962, than any of the self-incompatible populations. The average percentage of plants flowering in the eight undisturbed self-incompatible populations was 50 per cent; the average in the fifteen undisturbed self-compatible populations was five per cent. The difference is significant ($P<.001$) by a two-tailed 'Student's *t*' test. Furthermore, the percentage of plants flowering in each population is significantly correlated ($r=.77$, $P<.001$) with the logarithms of the number of flowers produced in 1962.

Thus the average number of plants, the estimated average number of flowers per plant, and the percentage of plants flowering in a population late in the flowering season are all correlated, and presumably determined by the same environmental factor, the drying of the soils in the spring. It is clear that the self-compatible populations in general occupy much poorer (drier) glade sites than those of the self-incompatible populations. As a number of the known and unknown glade sites have been excluded from the statistical comparisons and the comparison was made in only one year, there is a possibility that the association between self-compatibility and poor glade sites is fortuitous. Several additional considerations, however, strongly suggest

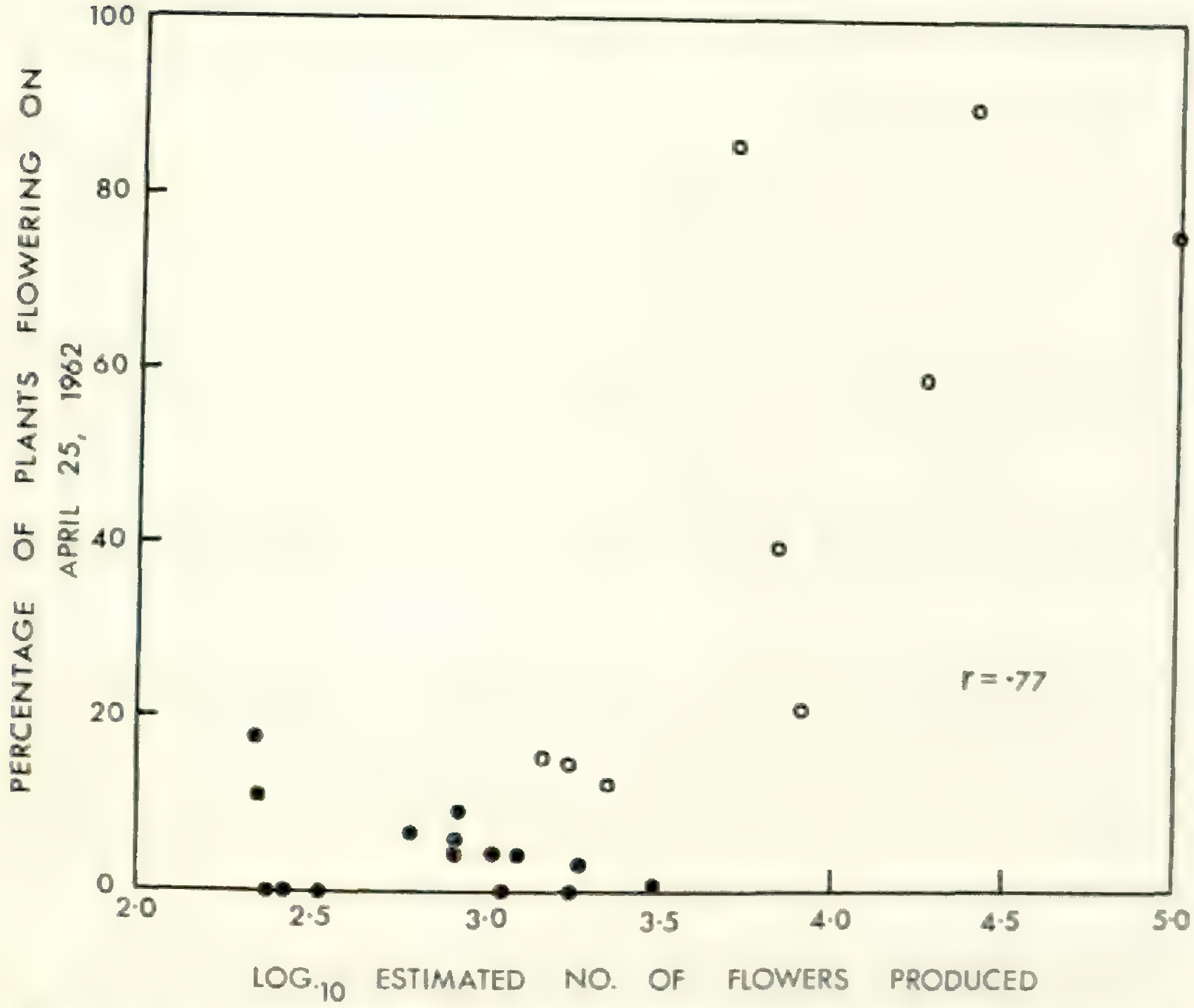


Fig. 17. The relationship between the estimated number of flowers produced in 1962 and the percentage of plants flowering on April 25, 1962, in the undisturbed glade populations of *L. crassa* and *L. alabamica*. Open circles represent self-incompatible populations; closed circles represent self-compatible populations.

that the association is a real phenomenon that bears on the evolution of self-compatibility.

First, the difference between self-incompatible and self-compatible populations is also apparent in the cultivated fields, where *Leavenworthia* continues to flower one to two weeks later than in the glades. Cultivated fields differ little in their soil moisture contents, and the later flowering of self-incompatible populations in cultivated fields may be partly genetically determined. This suggests that the more advanced races and species are adapted to earlier flowering, and presumably that they have lived under poor conditions, where earlier flowering is forced upon them, for a considerable time.

Second, I have observed the association between primitive breeding systems and later flowering in the species of *Leavenworthia* in Tennessee. *Leavenworthia stylosa*, the only self-incompatible species in Tennessee, continues flowering later than the other species in Tennessee. *Leaven-*

worthia uniflora, the species most adapted to autogamy, is the first to stop flowering in Tennessee. (This was also noted by Rollins, 1963).

The third line of evidence that the association between self-incompatibility and better glade sites has existed for a considerable time lies in a difference in the physiographic positions of the glades of self-incompatible and self-compatible populations. The glade sites of races a1, c2, c3 and c4 are the only known sites for self-incompatible races. The glades containing races a1, c2 and c4 in Franklin and Lawrence Counties occur in the Moulton Valley at some distance from the Pottsville escarpment, which marks the boundary between the Moulton Valley and Sand Mt. Plateau. These sites are on undulating to gently rolling ground, and many have permanent streams running through them. The glade sites of race c3 (self-incompatible) in the Massey-Lebanon district do not have streams running through them, but these glades are larger, and perhaps wetter, than those of other races in the Massey-Lebanon district.

The glade sites in the Massey-Lebanon district — most of the known glade sites of self-compatible races, as well as those of the self-incompatible race c3 — occur at the base or on the lower slopes of a line of low hills projecting from the Pottsville escarpment (maps 2 to 4). These hills are only 80 to 220 feet high and have few streams running from them. The glade sites are consequently much drier than those occupied by self-incompatible populations.

It is probably significant that the two most primitive races of the Massey-Lebanon district, races c3 and c5, are the farthest north in the area (farthest from the Pottsville escarpment) and at the lowest elevation (approximately 610 feet above sea level), while the most advanced race in both *L. crassa* and *L. alabamica,* races c15 and a4, occurs farthest south (closest to the Pottsville escarpment), and includes the populations at the highest elevation (approximately 680 feet above sea level).

Three self-compatible races — c6 and the 'Russellville' and 'Tuscumbia' races of *L. alabamica* — occur outside the Massey-Lebanon district. All of the known glade sites of the 'Tuscumbia' race are on the slopes of limestone hills in situations very similar to those occupied by the self-compatible races in the Massey-Lebanon district. Both race c6 and the Russellville race are known only from single field populations at the base of hills on the edge of the Moulton Valley.

Thus the nature of the glades of self-compatible populations is determined by physiographic features. At least for the races in the Massey-Lebanon district, there can be little doubt that these races have existed for some time under conditions similar to those existing today. The large number of *L. crassa* races in the Massey-Lebanon district can best be interpreted as meaning that the races of the Massey-Lebanon district have actually evolved in the area. There is a primitive, self-incompatible race (c3) of *L. crassa* in the Massey-Lebanon district, so the loss of self-incompatibility and concomitant changes in the Massey-Lebanon races of *L. crassa* have occurred in the Massey-Lebanon district, that is, while the populations were occupying poor glade sites similar to those occupied today.

It is possible that *L. alabamica* was already self-compatible before it reached the Massey-Lebanon district, since the two races of *L. alabamica* there are both self-compatible. But race a3 has an advancement index of only 30, so *L. alabamica* must also have been relatively primitive when it reached the Massey-Lebanon district. So most of the evolution of the features associated with self-compatibility in race a4 may also have occurred in the Massey-Lebanon district. Race c6, and the 'Russellville' and 'Tuscumbia' races of *L. alabamica* are each geographically isolated from other races of *L. crassa* and *L. alabamica*, and it is not known whether they evolved self-compatibility and other advanced characters before or after reaching the area they occupy at present.

The arguments presented above strongly suggest that the evolution of self-compatibility and concomitant changes in other characters are associated with the nature of the glades. It appears that on several separate occasions populations of *L. crassa* and *L. alabamica* came into hilly areas, where the glades are poorer. As a consequence the populations in these areas have fewer plants, with fewer flowers per plant, and flowering is completed earlier. In the following sections evidence is presented that the changes in the breeding system have actually taken place in response to a relative paucity of insect pollinators in the earlier flowering populations of the poorer glade sites.

THE POLLINATION OF LEAVENWORTHIA FLOWERS

It has been frequently suggested that self-compatibility has arisen in various plants under conditions where there are relatively few suitable insect pollinators, or when the pollinators are unable to effect sufficient pollination, for example when there is frequent bad weather. Unfortunately there are very few circumstances in nature where this hypothesis can be tested. Most self-compatible taxa have arisen long ago, or have spread from the area in which they originated, so that their present ecological conditions may not closely resemble those under which they arose. And in many self-compatible plants other changes have followed the acquisition of self-compatibility, and have resulted in a lesser attractiveness of the flowers to their natural pollinators, so that even if there are close self-incompatible relatives still existing, insect visits to the two groups are not strictly comparable.

Leavenworthia alabamica, and particularly *L. crassa,* offer an unusually favorable opportunity for an investigation of the selective factors producing self-compatibility. Self-incompatible and self-compatible races exist in both species, and the pattern of distribution of the races, particularly those of *L. crassa* in the Massey-Lebanon district, suggests that the self-compatible races have arisen recently under conditions closely approximating those existing in the cedar glades today. Moreover, in both species the flowers of the more primitive self-compatible races differ appreciably from their self-incompatible relatives only in the ease of self-fertilization, and may therefore be assumed to be equally attractive to insects.

For these reasons detailed studies of the numbers of the various insect visitors to *Leavenworthia* flowers, and their manner of operation, were made during the 1961 and 1962 flowering seasons. To reduce the possibility that any differences in the insects on each population were caused by racial differences in the attractiveness of the flowers, or to geographical differences in the pollinators available, the detailed comparisons of the populations have been restricted to glade populations which belong to large-flowered races of *L. crassa* in the Massey-Lebanon district, and occupy sites which have not been appreciably disturbed by agricultural practices. In addition, supplementary observations were made on glade populations of *L. crassa* and *L. alabamica* outside the Massey-Lebanon district, on glade populations of *L. stylosa* in Tennessee (1961 only), and on cultivated populations of *L. crassa* and *L. alabamica.*

It quickly became apparent that there is a considerable variety of insects visiting *Leavenworthia* flowers. Collections of insects on both *L. crassa* and *L. stylosa* were made on a number of occasions (in 1961 and 1962 on *L. crassa*, in 1961 only on *L. stylosa*). A list of the species collected and later identified by specialists in the appropriate groups is given in table 11. Many of the species were collected only once, and undoubtedly additional species which visit *Leavenworthia* flowers less frequently would have been added if larger collections had been made.

All the bees collected, except the honeybee, are nonsocial and native to the eastern United States. Apart from special attempts to catch the most easily distinguished species, the collections of the native bees were made more or less randomly by my attempting to net the closest bee on each occasion. The numbers of the native bee species caught are therefore a rough indication of their relative abundance. This is not so for the other insects, each of which was caught after a special search.

A considerable number of counts of the various insect visitors on glade and field populations of *Leavenworthia* was made in 1961 and 1962 (table 12). To count the insects, I moved slowly and cautiously over a population, noting only those insects actually on the *Leavenworthia* flowers, and apparently feeding or collecting pollen. Occasional insects merely resting on the flowers (mostly Diptera) were omitted from the counts. Honeybees, native bees, and non-Hymenoptera were counted separately. The small black beetle, *Meligethes nigrescens* Stephens was very common on *Leavenworthia* flowers, but it never moves between flowers during the day and probably achieves very little pollination, so it was excluded from the counts.

In counting the insects on the glade populations (except population 89) I walked once over the whole population,

TABLE 11. LIST OF INSECTS COLLECTED ON L. CRASSA AND L. STYLOSA FLOWERS

Order	Family	Genus and Species	Number collected	Leavenworthia species
Hymenoptera				
	Colletidae	*Hylaeus modestus* Say	1	*L. stylosa*
	Andrenidae	*Andrena arabis* Rob.	7	*L. crassa*
		A. bisalicis Vier.	1	*L. stylosa*
		A. cressonii Rob.	3	*L. crassa*
		A. (near) *erythronii*	1	*L. stylosa*
		A. ? *nothoscordi* Rob.	16	*L. crassa*
		A. personata Rob.	2	*L. crassa*
		A. platyparia Rob. (♂)	1	*L. crassa*
		A. violae Rob.	1	*L. crassa*
		A. (near) *ziziae*	4	*L. stylosa*
	Halictidae	*Halictus confusus* Sm.	1	*L. crassa*
		H. ligatus Say	2	*L. crassa*
		Dialictus amirandus (Sandh.)	5	*L. stylosa*
		D. anomalus Rob.	2	*L. crassa*
		D. apocyni Mitch.	1	*L. crassa*
		D. inconspicuus (Sm.)	5	*L. crassa*
		D. tegularis (Rob)	1	*L. crassa*
		D. versatus (Rob.)	1	*L. crassa*
		D. zephyrus (Sm.)	1	*L. crassa*
		Augochlora pura Say	1	*L. crassa, stylosa*
		Augochorella aurata (Sm.)	13	*L. crassa, stylosa*
	Megachilidae	*Osmia conjuncta* Cress.	2	*L. crassa*
	Apidae	*Nomada* sp.	1	*L. crassa*
		Ceratina calcarata Rob.	1	*L. crassa*

		C. metallica Sm.	15	*L. crassa*
		Apis mellifera L. (introduced)	10	*L. crassa, stylosa*
Diptera				
	Stratiomyidae	*Labostigma* sp.	3	*L. crassa*
	Bombyliidae	*Bombylius major* L.	5	*L. crassa*
	Syrphidae	*Chrysogaster nitida* Wied.	1	*L. crassa*
		Helophilus fasciatus Walker	7	*L. crassa*
		H. latifrons Loew	1	*L. crassa*
		Metasyrphus americanus (Wd.)	1	*L. crassa*
		Mesograpta marginata (Say)	15	*L. crassa*
		Taxomerus geminatus (Say)	3	*L. crassa*
Lepidoptera				
	Pieridae	*Anthocaris genutia* Fab.	6	*L. crassa, stylosa*
		Colias eurytheme Bois.	1	*L. crassa*
		Eurema nicippe Cramer	1	*L. crassa*
	Nymphalidae	*Vanessa virginiensis* Drury	3	*L. stylosa*
	Lycaenidae	*Lycaena phloeas* L.	1	*L. stylosa*
		Mitteura gryneus Hueb.	1	*L. crassa*
	Hesperiidae	*Thanaos* sp.	2	*L. crassa*
	Sphingidae	*Hemaris diffinis* Bois.	1	*L. stylosa*
	Euchromiidae	*Cisseps fulvicollis* Hüb.	1	*L. stylosa*
	Noctuidae	*Caenurgia ? erechtea*	1	*L. crassa*
	Thyrididae	*Thyris lugubris* Bois.	3	*L. crassa*
Coleoptera				
	Nitidulidae	*Meligethes nigrescens* (Steph.)	36	*L. crassa*

Insects collected on *L. crassa* are from Lawrence and Morgan counties, Alabama. Insects collected on *L. stylosa* are from Rutherford and Wilson counties, Tennessee.

and attempted to glance briefly at every flower. Ideally this method enables every insect working on the *Leavenworthia* flowers of one glade population at one time to be observed and counted. The numbers observed are probably somewhat below the true figures however, as even a slow movement over the population must distract the insects to some extent, particularly those approached while flying between two flowers. And although all the insects are easily seen on the light-colored background provided by the *Leavenworthia* flowers, a small percentage of the insects on the flowers was probably overlooked. Glade population 89 (race c3) and populations on cultivated fields were too large to examine completely for insect visitors, and the counts represent the samples of insects seen while I walked over a portion of each population.

Most populations on which the insects were counted were observed on several occasions in either 1961 or 1962; only a few populations had insect counts made on them in both 1961 and 1962. Table 12 shows the number and percentages of honeybees, native bees and non-Hymenoptera in the counts on each population of *L. crassa* and *L. stylosa* in 1961 and 1962.

Considering all of the insect visitor counts on *L. crassa* and *L. stylosa* in 1961 and 1962, a total of 2432 insects was observed during 127 separate counts on 23 populations of *L. crassa* and 9 populations of *L. stylosa*. Of the insects observed, 1393 (57 per cent) were honeybees, 686 (28 per cent) were native bees, and 353 (15 per cent) were non-Hymenoptera. The relative proportions of honeybees and native bees were similar in the 1961 and 1962 counts, including those on populations 37, 88, 89, 100, and 171 on which insect counts were made in both years.

Non-Hymenoptera constituted less than a quarter of the insects counted on most populations in both 1961 and 1962, but made up as much as 37 per cent of the insect visitors (population 37 in 1961). Table 12 shows that the percentage of non-Hymenoptera was generally higher in the 1961 counts on *L. crassa* populations than in the 1962 counts. This is principally due to the fact that there were many more individuals of the *Helophilus* species observed in 1961 than in 1962 (Lloyd, 1964). There were also differences between geographical areas in the species of non-Hymenoptera observed. For example, *Bombylius major* and the *Helophilus* species were common on *L. crassa* in Morgan and Lawrence counties, Alabama, in 1961 and 1962, but were not found on *L. stylosa* in Tennessee.

Although there are appreciable numbers of honeybees, native bees, and non-Hymenoptera on both glade and cultivated populations, it is apparent that their relative proportions are very different in glade and field populations. In all 12 field populations of *L. crassa* which were counted in 1961 and/or 1962 there were more than three times as many honeybees as native bees. But in the 12 glade populations of *L. crassa* (excluding population 89) and *L. stylosa* the situation is completely reversed; there were more than twice as many native bees as honeybees in every case, and the honeybees were outnumbered by as much as 23:1 (population 38). There is no doubt that the difference in proportions of honeybees and native bees between undisturbed glade and field populations is quite general, and is not based on one or two anomalous populations. The pollinators on population 89, which has been greatly disturbed by the removal of forest around its margin, are more similar to those on the field populations than those on other glades.

There are, I believe, two possible explanations for the higher proportion of honeybees on field population. Glade and field populations differ in their size, and in the nature of their soils and surrounding vegetation. It is well known that honeybees are attracted to large masses of flowers, and that foragers returning to the hive may transmit information about good foraging sites to other bees, thus stimulating an increased activity on a favored population. The field populations, and population 89, are much larger than the glade populations, and may attract relatively more honeybees for this reason.

This alone cannot explain the higher percentage of honeybees on field populations, however; if the population size is the controlling factor it is necessary to postulate that the native bees are less influenced by the size of a population than honeybees are. There is no evidence that there is any relationship between the size of a population and the relative numbers of honeybees and native bees, either in the glade or in the field populations. Amongst the field populations there are most native bees (relative to the number of honeybees)

TABLE 12. INSECT COUNTS ON POPULATIONS OF L. CRASSA AND L. STYLOSA IN 1961 AND 1962

Species and Race	Population	Description of site	Date of counts (April)	No. of counts	Total no. of honeybees	Percentage of Honeybees	Total no. of native bees	Percentage of native bees	Total no. of non-Hymenoptera	Percentage of non-Hymenoptera	Total no. of insects
			1961 COUNTS								
L. crassa											
		Massey-Lebanon district, Morgan Co., Alabama.									
Race: c3	89	disturbed glade	3-18	7	108	61.4	29	16.5	39	22.2	176
c3	87	corn field	3-18	10	142	52.0	30	11.0	101	37.0	273
c3	88	corn field	3-18	7	124	66.7	23	12.4	39	21.0	186
c5	58	corn field	5-18	3	29	60.4	8	16.7	11	22.9	48
c5	69	corn field	5-18	2	37	82.2	5	11.1	3	6.6	45
c5	100	unploughed field	18	1	35	97.2	1	2.8	0	0.0	36
		Other districts, Morgan and Lawrence counties, Alabama.									
c1	170	corn field	7-11	2	81	88.0	3	3.3	8	8.7	92
c1	171	field with forest remnants	7-11	2	63	52.5	18	15.0	39	32.5	120
c4	46	corn field	7	1	18	60.0	7	23.3	5	16.7	30
c6	268	corn field	18	1	28	73.7	5	13.2	5	13.2	38
L. stylosa											
		Several counties, Nashville Basin, Tennessee.									
	total for 9 populations	glades, some disturbed	23-24	11	23	8.7	206	78.0	35	13.3	264

L. crassa

1962 COUNTS

Massey-Lebanon district, Morgan county, Alabama.

Race: c3	89	disturbed glade	6-21	9	207	74.5	52	18.7	19	6.8	278
c3	743b	glade	9-21	6	23	28.4	49	60.5	9	11.1	81
c3	743c	disturbed glade	9-21	6	10	22.2	31	68.9	4	8.9	45
c3	743a	glade	9-21	8	6	14.6	32	78.0	3	7.3	41
c3	743e	glade	9-21	5	4	28.6	9	64.3	1	7.2	14
c11	742	glade	9-21	5	1	6.7	11	73.3	3	20.0	15
c5	86	glade	9-21	6	3	12.0	22	88.0	0	0.0	25
c5	791	glade	14-21	4	0	0.0	5	83.3	1	17.0	6
c3	743d	glade	9-21	6	0	0.0	3	75.0	1	25.0	4
c5	118a	glade	9-21	4	0	—	0	—	0	—	0
c3	37	corn field	6-21	5	188	75.8	49	19.8	11	4.4	248
c3	88	corn field	14-19	3	76	79.2	17	17.7	3	3.1	96
c3	748	grazed field	14	1	18	78.3	4	17.4	1	4.4	23
c5	100	unploughed field	6- 9	2	25	83.3	2	6.7	3	10.0	30
c5	59	corn field	6-21	4	120	87.0	12	8.7	6	4.0	138

Other districts, Morgan and Lawrence counties, Alabama.

c4	38	glade	25	1	2	3.9	46	90.2	3	5.9	51
c1	171	field with forest remnants	22	1	22	75.9	7	24.1	0	0.0	29

on population 46, yet this is one of the largest populations on which the insects were counted. Also, populations 59, 69, and 100 had relatively fewer native bees than other field populations, but populations 69 and 100 were rather small field populations, while population 59 was a large population.

It seems much more likely that the difference in the visitors to the glade and field populations is due to the position or nature, rather than the size, of the sites the populations occupy. The fact that the disturbed glade population 89 has proportions of honey and native bees closely resembling those on the field populations suggests that it is the surroundings of a population that determine the relative numbers of honeybees and native bees. The glade site of population 89 is quite similar to that of the other glade populations except for having most of the forest removed from its margins, and is totally different from the fields occupied by *Leavenworthia*.

Most of the native bees collected are ground-nesting species, which cannot complete their life cycle in nests in ploughed land (Malyshev, 1936). On the other hand the glades themselves and the forest which surrounds them provide suitable habitats for the nests of both ground-nesting and wood-nesting bees. The cedar glade populations of *Leavenworthia* are closer to the nesting sites of the native bees than are the field populations. It is known that bumblebees and at least some solitary bees prefer to forage close to their nests (Free and Butler, 1959; Linsley, 1958). Braun *et al.* (1956) have shown that bumblebees are more or less evenly dispersed over small clover fields, but in large fields the number of bees decreases from the edges of the field. If the native bees visiting *Leavenworthia* also prefer to forage close to their nests, this would explain their lower percentages on cultivated populations. The honeybees would not be similarly affected since they have to fly some distance to both the glade and field populations.

Population 89 (on a disturbed glade) and populations 37 and 88 (in corn fields) are less than 50 yards from the margin of the forest containing glade populations 743 and 791. All of these populations are probably visited by honeybees from the same hives and yet there are many fewer native bees (relative to the number of honeybees) in the disturbed glade and corn field populations. Apparently the native bees do not often fly even this short distance onto the cultivated fields.

The differences between the various field populations in the proportions of honeybees and native bees appear to agree with the hypothesis that the distance from the nesting sites is largely controlling the number of native bee visitors to a *Leavenworthia* population. Amongst the field populations the number of native bees most nearly approaches the number of honeybees in populations 46 and 171: population 46 is adjacent to a stream with waste land along the margins, and population 171 is in a field which had not been completely cleared of forest. And populations 59, 171, and 100, which have the lowest percentages of native bees, are the farthest from any forest.

It is obvious from the above discussions that the introduction of the honeybee and the spread of *Leavenworthia crassa* onto cultivated land have had considerable effects on the abundance of the insect visitors to *L. crassa* populations. With regard to the introduction of the honeybee into North America, Pearson (1933) states that "this introduced species appears to exert an influence upon native bees which is visible to any student of the native species. So efficient is it as a collector of pollen and honey and so ubiquitous has it become, there can be no question but what its inroads cause a serious diminution in the food supply of native bees, particularly in bad seasons." Fortunately, this effect has been much greater in the field populations of *Leavenworthia* than in the glade populations. It may be that the development of extensive field populations of *L. crassa* close to the glade populations has minimized the effect of the honeybee in the glades by offering alternative, much larger, populations for the honeybees to use. All of the glade populations of *L. crassa* (except population 89) on which insects were counted have been little disturbed by human activities, and it seems likely that apart from the introduction of the honeybee, the plant-pollinator relationships in these 'undisturbed' glades of *L. crassa* are similar to those under which the races differentiated.

THE RELATIVE EFFECTIVENESS OF DIFFERENT INSECTS AS POLLINATORS

The figures given above suggest that although native bees are the predominant natural insect visitors, the non-Hymenoptera play an appreciable role in the pollination of *Leavenworthia* flowers. Considerations of the structure of *Leavenworthia* flowers, the mode of action of the Hymenoptera and non-Hymenoptera visiting the flowers, and a comparison of the rapidity of the movements of Hymenoptera and non-Hymenoptera indicate, however, that the non-Hymenoptera are much less important than their frequency would suggest.

The flowers of *Leavenworthia* are erect; the petal claws are also erect and appressed to the circle of filaments which closely surround the pistil (fig. 3). The petal limbs bend at right angles to the claws in fine weather and thus form a horizontal platform. The stigma projects approximately 1 mm above the outspread petal limbs, and is closely surrounded by, and sometimes completely concealed within, the anthers of the four paired stamens. In the more primitive races, including all of those on which the pollinators were studied, the anthers of the paired stamens face obliquely or directly away from the stigma and the pollen is freely exposed to insect visitors. The single stamens are more or less strongly curved in the open flower and their anthers lie slightly below the level of the petal limbs. Consequently there is a narrow channel on either side of the flower, enclosed by a single anther, the adjacent petal claw margins and the filaments of the paired stamens. These spaces lead to the nectaries at the base of the anthers, and may therefore be called nectar channels. Their length and width vary somewhat between the races, and with the vigor of the plant, but they are approximately 5 mm deep, and less than 1 mm in diameter.

Leavenworthia flowers thus have completely concealed nectar and exposed anthers (those of the paired stamens) surrounding the stigma in a cone in the center of, and slightly above, the outspread petal limbs. According to Knuth (1906, page 20), H. Müller claimed that "it may be . . . correct that in all . . . flowers in which the anthers are borne upon short, stiff filaments, and enclose the conical style, bees are the necessary agents of cross-pollination." This arrangement is rather uncommon in the *Cruciferae*, most of which have only partly concealed nectar, but it is common within the *Compositae*. Müller (1883, page 581) summarizes the insects he noted on 25 *Compositae* species; the insect groups and their relative frequencies on these species are very similar to those observed on *Leavenworthia.*

The majority of the native bees land on or climb onto the central cone containing the stigma and the anthers of the paired stamens and crawl rapidly over or "wallow" (Malyshev, 1936) on the cone. Their actions are usually very vigorous and there is little doubt that they often succeed in separating the anthers and touching the stigmas, and at the same time in picking up abundant pollen on their legs and undersides. Most of the native bees appeared to collect both pollen and nectar, although some of the smaller bees made no attempt to insert their proboscises into a nectar channel, possibly because the nectar was too deeply concealed.

The action of the honeybees in visiting the flowers of *Leavenworthia* is very different from that of the native bees. A honeybee lands on one of the petal limbs, with its head towards the center of the flower. Its weight causes the pedicel of the flower to bend over and the honeybee grasps the petals with its legs while it quickly inserts its head into the top of one or both of the nectar channels. In doing so the petals and the single anther surrounding the nectar channel are forced apart, and the bee's head is brought against the paired stamens and the pistil. The forceful actions of a honeybee presumably result in a considerable amount of cross-pollination.

All of the honeybees visiting *Leavenworthia* flowers appeared to be seeking nectar, for they invariably pushed their heads into one or both of the nectar channels. Many of the honeybees seemed to be collecting pollen, too, for the pollen baskets of most honeybees foraging on *Leavenworthia* contain pollen. Samples of the pollen masses from two honeybees collected on *L. crassa* were examined and proved to contain cruciferous pollen, presumably that of *Leavenworthia.*

The actions of the non-Hymenopteran species are such that they rarely or never touch the stigmas. *Bombylius major* and the Lepidoptera species stand on the petal limbs with their heads above the nectar-channels but they are able to reach the nectar without putting their heads close to the entrance of the nectar-channels, and thus they do not usually come into contact with the anthers of the paired stamens.

If they do touch the paired stamens they probably rarely do so with sufficient force to separate them and touch the stigma. Müller (1883, page 580) notes that butterflies are often quite useless as pollinating agents in their visits to bee flowers, and this seems to be the case in *Leavenworthia.*

The remaining species of non-Hymenoptera (chiefly Diptera and Coleoptera) feed on the exposed pollen of *Leavenworthia* flowers. The species of Syrphidae are the principal pollen feeding insects. The syrphids stand on the petal limbs and take pollen from the anthers of the paired stamens. They may cause some pollen to be scattered onto the stigmas of the same flower, but as Robertson (1924) notes, they are light and rest so superficially on the flowers that they can eat the pollen without carrying it on their bodies, and are therefore useless as pollinators of flowers with exposed pollen.

The importance of the Hymenoptera in the pollination of *Leavenworthia* is even clearer when the time the various insects spend on a single flower is considered. Individuals of all the major groups of insect visitors were followed for some time, while the number of flowers and the time they took to visit them were noted (table 13).

In both 1961 and 1962 several individuals of *Apis mellifera* spent an average of almost exactly 4 seconds on each

TABLE 13. AVERAGE TIME INSECTS SPENT ON L. CRASSA FLOWERS

Order	Species	Year	No. of insects timed	No. of flowers visited	Total time (seconds)	Av. time on each flower (seconds)
Hymenoptera	*Apis mellifera*	1961	5	260	1060	4.08
		1962	7	383	1510	3.94
	Halictus ligatus[1]	1962	1	65	535	8.23
	Andrena cressonii..	1962	1	89	630	7.08
	Andrena ?nothoscordi[1]	1962	1	40	430	10.75
	Ceratina metallica[1]	1962	1	12	135	11.25
	Species unknown	1962	1	18	105	5.83
	Species unknown	1962	1	26	150	5.77
	Species unknown	1962	1	40	430	10.75
	Species unknown	1962	1	129	1060	8.22
Diptera	*Bombylius major*	1961	2	52	310	5.96
		1962	1	58	310	5.35
Lepidoptera	*Anthocaris genutia*	1962	3	214	1615	7.55
	Thyris lugubris	1962	1	13	190	14.62
	Caenurgia ?erechtea	1962	1	16	915	57.19

[1] Individual collected after it was timed. The species of Syrphidae (Diptera) and Nitidulidae (Coleoptera) were not timed. The syrphids spent up to several minutes on each flower, and the nitidulids were never seen moving from one flower to another during the day.

flower. Individuals of several species of native bees spent between 5.77 and 11.25 seconds on each flower. It appears that there are differences between the native bee species in their speed of operation, but that all spend somewhat more time on each flower than do honeybees.

No accurate timings of the syrphid species were taken; they nearly all spend a long time on each flower (often several minutes) and they rest for considerable periods either on the ground or on a flower after relatively few flower visits. *Bombylius major*, on the other hand, moves almost as quickly from flower to flower as honeybees do. The Lepidoptera species vary tremendously in the rapidity of their movements from flower to flower, but on the whole they are comparatively slow workers.

When the structure of *Leavenworthia* flowers is considered together with the mode and speed of action of the various insect visitors there is no doubt that the bees are the only significant pollinators of *L. crassa* and *L. stylosa* flowers. They probably achieve 99 per cent or more of the cross-pollinations and a considerable proportion of the self-pollinations of *L. crassa* and *L. stylosa* flowers.

THE EFFECT OF POPULATION SIZE ON THE NUMBER OF POLLINATORS

It was shown above that glade populations of *L. crassa* and *L. alabamica* differ considerably in their size, and that in general the self-compatible races have relatively small glade populations which cease flowering earlier than the larger glade populations of self-incompatible races. Furthermore, self-compatibility has apparently arisen under glade conditions similar to those of the self-compatible races today. It is possible therefore that self-compatibility may have arisen in response to a paucity of insect visitors to small, early-flowering glade populations.

To examine the effect of population size on the number of pollinators it is necessary to have estimates of both the number of pollinators foraging on a series of populations and the number of flowers in those populations. The number of pollinators divided by the number of flowers (i.e. the fraction of flowers with pollinators on them at any one time) gives an estimate of the relative abundance of pollinators.

The counts on the glade populations of *L. crassa* (except population 89) were made by observing the insects on all the flowers of a population. Since the populations were small and could be examined sufficiently quickly that there was little possibility of counting an insect more than once in one count, the number of insects counted may therefore be taken as the number on a population at any one time. The insect counts on the undisturbed glade populations of *L. crassa* were made between the 9th and the 21st of April 1962. On April 16, 1962, the number of flowers in each glade was counted (table 14). These numbers may be taken as estimates of the average number of flowers in the glades throughout the period when the insects were counted.

The non-Hymenoptera are not important pollinators of *Leavenworthia* flowers, so these have been excluded from the calculations of the relative numbers of pollinators in each population. The average number of honeybees seen on one count of each glade population was then divided by the number of flowers in the same population on April 16, 1962, to give an estimate of the fraction of flowers with honeybees on them at any one time when bees were active throughout the period of the counts (table 14). Similarly the average number of native bees per count divided by the number of flowers gives an estimate of the fraction of flowers in each population with native bees on them at any one time. It should be emphasized that the counts were made only on fine days between 10 AM and 3 PM, when the bees were fully active.

The results show that there were between 0 and 0.22 per cent of the flowers with honeybees on them at one time in the various glade populations, and between 0 and 1.62 per cent of the flowers with native bees on them. That is, only a very small fraction of the flowers have bees on them at any one time.

The calculations of the speed of movement of honey and native bees from flower to flower may be combined with the fraction of flowers with bees on them at one time to give an estimate of the number of bees which, on the average, visit each flower in a given time. Then if the time each flower is open while the bees are foraging is known one can obtain finally an estimate of the average number of bees which visit a flower in the various glade populations.

For this purpose, it was considered that a honeybee takes 4 seconds to go from flower to flower. The native bees vary considerably in the rapidity with which they move from flower to flower (table 12). For the purposes of the subsequent calculations, it was considered that a figure of 8 seconds per flower would be a reasonable estimate for the native bees as a whole.

The majority of the flowers remain open for only one fine day. If a flower is not pollinated on the first day it may, however, remain open for a second, or even a third day. Moreover, if a flower becomes ready to open on a cold, dull or rainy day it may remain closed for one or two days until the weather improves sufficiently for it to open. The weather conditions necessary for bee flight and for *Leavenworthia* flowers to open are quite similar; in general if the flowers open, the bees are more or less active, and vice versa.

On a fine, warm day in the middle of April the bees become active at approximately 9 AM, and forage until about 3 PM. Although there is considerable variation from day to day in flower and insect periodicity it seems reasonable to say that on the average a single *Leavenworthia* flower is open for approximately 6 hours when the bees are active.

If a honeybee were to forage continuously for 6 hours it would visit $\frac{60}{4} \times 60 \times 6 = 5400$ flowers; a native bee would visit $\frac{60}{8} \times 60 \times 6 = 2700$ flowers. Of course one bee does not forage continuously for 6 hours, but the average number of visits to a single flower is equal to the fraction of flowers with bees on them at any one time multiplied by the number of flowers that a single bee would visit if it were active throughout the time that a flower is open.

The estimated number of honeybees and native bees that on the average visited a flower in each of the glade populations studied is given in table 14, together with the total (honeybee plus native bee) visits per flower. There is considerable variation between populations in the estimates for both the number of honeybees and the number of native bees which visit each flower. The estimated number of honeybees visiting each flower ranges from 0 for populations 118a, 791 and 743, to 11.9 for population 86. The

TABLE 14. ESTIMATED NUMBER OF BEES VISITING EACH FLOWER IN GLADE POPULATIONS OF L. CRASSA IN 1962

			Av. no. of bees in each count[2]		Fraction of flowers with bees on		Estimated no. of bees visiting each flower[3]		
Race	Population	No. of flowers April 16[1]	No. of honeybees	No. of native bees	Fraction with honeybees	Fraction with native bees	No. of honeybees	No. of native bees	Total No. of bees
c3	743b	3500	3.83	8.17	1.09×10^{-3}	2.33×10^{-3}	5.9	6.3	12.2
c3	743c	1610	1.67	5.20	1.04×10^{-3}	3.23×10^{-3}	5.6	8.7	14.3
c3	743a	856	0.75	4.00	0.87×10^{-3}	4.67×10^{-3}	4.7	12.6	17.3
c3	743e	631	0.80	1.80	1.27×10^{-3}	2.85×10^{-3}	6.9	7.7	14.6
c11	742	251	0.20	2.20	0.80×10^{-3}	8.77×10^{-3}	4.3	23.7	28.0
c5	86	226	0.50	3.67	2.21×10^{-3}	16.23×10^{-3}	11.9	44.3	56.2
c5	791	215	0.00	1.20	0.00	0.56×10^{-3}	0.0	1.5	1.5
c3	743d	185	0.00	0.50	0.00	0.27×10^{-3}	0.0	0.7	0.7
c5	118a	134	0.00	0.00	0.00	0.00	0.0	0.0	0.0

[1] These figures are taken as the average number of flowers present during the period when the insects were counted (April 9 to April 21, 1962).

[2] The raw data for these figures is given in table 12. These figures are taken as the average number of bees on each population at any one moment.

[3] Each flower is assumel to be open for one day, during which the bees are foraging for 6 hours.

estimated number of native bees visiting each flower ranges from 0 for population 118a to 44.3 for population 86. The estimated total number of bees visiting each flower ranges from 0 for population 118a to 56.2 for population 86.

At this point I must emphasize that these figures are based on four parameters — the number of flowers in a population, the number of bees foraging on a population at one time, the speed of movement of the bees from flower to flower, and the time that each flower is available for insect visits. All of the four component figures are approximate only, so there may be considerable error in any one of the final figures. In general, however, the errors are likely to be in the same direction for all populations.

Even if these figures are incorrect by a factor of two or three there can be no doubt that each flower is visited by only a small number of bees. And these calculations refer only to those flowers which are open on fine warm days. In the early part of the flowering season particularly there may be several successive days during which there are no suitable foraging conditions, or only short periods when the bees are active. Flowers which are ready to open at such times may never open fully and receive any insect visits. That this is so is demonstrated by the fact that a small proportion (up to 16 per cent) of the fruits collected from samples of the glade plants are aborted, i.e. were never pollinated. And this is in spite of the fact that a considerable number of flowers must be self-pollinated without the aid of insects.

The glade populations on which the numbers of bees visiting each flower were estimated are arranged in Table 14 in order of the number of flowers present on April 16, 1962. The number of flowers ranged from approximately 3500 in population 743b to 134 in population 118a. It is apparent that there is no consistent trend in the estimated number of honeybees and native bees visiting each flower from the population with the largest number of flowers to the population with the smallest number of flowers, although the three smallest populations received many fewer bee visits to each flower than the other populations.

The high figure for population 86 is probably due to the fact that this population experienced a greater decline in the number of flowers during the period of the insect counts than did the other populations. Since the number of flowers was counted on April 16, in the latter half of the period of the insect counts, the average number of flowers throughout this period was probably greater than the number observed on April 16. Consequently the average number of bees visiting each flower of population 86 has been overestimated. There is a similar source of error in the estimations for the other populations, but the number of flowers in them declined much more gradually than in population 86, and the error is accordingly much smaller.

The large differences between the three populations with the fewest flowers (791, 743d, and 118a) and the remaining glade populations in the number of honey and native bees visiting each flower probably represent a true difference between the larger and smaller glades. I noted on several occasions other than those of insect counts that there were no bees on the smaller glade populations. The three smallest populations, however, differ little in size from populations 742 and 86, which received many more bee visits. Perhaps smaller populations do not necessarily attract relatively fewer bees, but for some reason are less likely to be visited frequently; their smaller size or shallower soils in the surrounding forest may decrease the chance that there are suitable nesting sites in their immediate vicinity.

POLLINATOR CHANGES DURING A FLOWERING SEASON

The counts of the number of bees visiting the *Leavenworthia* populations were also examined to see if there were any significant changes in the course of a flowering season. The number of bees visiting *Leavenworthia* flowers in the early and late parts of the flowering season would ideally be compared by studying the number of bees visiting each flower in the early and late flowering periods of the glade populations. Unfortunately my data are not sufficiently extensive for a direct comparison to be made in this way — the number of flowers in each undisturbed glade population was counted only once, and the insect counts were not begun until the peak of the flowering period.

It was noticed, however, that the ratio of native bees to honeybees appeared to increase throughout the flowering season, on both glade and field populations of *L. crassa* in 1961 and 1962. This observation was examined more closely by dividing the 1961 and 1962 insect counts on *L. crassa* populations into those made in the first half of the period of the insect counts in each year, and those made in the second half of this period.

In 1961 the insect counts on *L. crassa* populations were made between April 3, when flowering was at its peak, and April 18 when flowering had almost ceased. Counts made from April 3 to April 8 are considered to have been made in the mid-flowering period, and those made between April 11 and April 18 are considered to have been made in the late-flowering period. No counts were made on April 9 and 10.

The 1962 counts were made between April 6 and April 21. Those made between April 6 and April 10 are considered to have been made in the mid-flowering period, though the number of flowers was beginning to decline at this time; those made between April 14 and April 21 are considered to have been made in the late-flowering period.

The number of native bees divided by the number of honeybees in each population, in the mid- and late-flowering periods, is shown in table 15 for those populations on which

TABLE 15. COMPARISON OF BEES VISITING L. CRASSA POPULATIONS DURING MID-FLOWERING AND LATE-FLOWERING PERIODS IN 1961 AND 1962

Race	Population	Flowering Period	No. of counts	Total no. of honeybees	Total no. of native bees	No. of native bees / No. of honeybees
		1961, glade population				
c3	89a	middle	3	77	7	0.09
		late	3	31	22	0.71**
		1961, field populations				
c3	37	middle	3	87	12	0.14
		late	4	55	18	0.33*
c3	88	middle	3	71	5	0.07
		late	4	53	18	0.34**
c5	58	middle	1	14	2	0.14
		late	2	15	6	0.40
c5	69	middle	1	15	1	0.07
		late	1	22	4	0.18
		1962, glade populations				
c3	89	middle	5	157	18	0.12
		late	4	50	34	0.68**
c3	743b	middle	1	6	12	2.00
		late	5	17	37	2.12
c3	743c	middle	2	8	7	0.88
		late	4	2	24	12.00**
c3	743a	middle	2	3	4	1.33
		late	6	3	28	9.33
c3, c5, c9	6 glades[1]	middle	12	7	28	4.00
		late	18	1	22	22.00
		1962, field populations				
c3	37	middle	3	166	39	0.24
		late	2	22	10	0.56
c5	58	middle	2	88	0	0.00
		late	2	32	12	0.38**

[1] The data from populations 743e, 742, 86, 791, 743d and 118a was grouped to obtain a sufficient number of observations for comparison of the two periods.

*The ratio of native bees to honeybees was significantly higher ($P = .05 - .01$) in the late-flowering period than in the mid-flowering period.

**The ratio of native bees to honeybees was significantly higher ($P < .01$) in the late-flowering period than in the mid-flowering period.

a sufficient number of insects were counted in 1961 or 1962 for a comparison of the two periods to be made. In addition the 1962 counts on six smaller glade populations on which only a few bees were observed have been pooled to obtain sufficient numbers for the comparison. In all twelve possible comparisons the ratio of the number of native bees to the number of honeybees is greater in the late-flowering period than in the mid-flowering period. The difference is significant (P$<$.05) for six populations; the lack of significant differences in the other populations can be attributed principally to the small number of observations.

Considering the totals from the six populations observed in both periods in 1961, in the mid-flowering period the ratio of native bees to honeybees was 27:264 or 0.10:1, and in the late-flowering period the ratio was 68:176 or 0.39:1. Thus compared with the number of honeybees, there were $0.39/0.10 = 3.78$ times as many native bees in the late-flowering period as in the mid-flowering period. The mid-points of the mid- and late-flowering periods were only 9 days apart, so a large change in the proportions of native bees and honeybees occurred in a very short time.

Considering the totals from the eleven populations observed in both periods in 1962, the ratio of native bees to honeybees was 108:435 or 0.25:1 in the mid-flowering period and 167:127 or 1.31:1 in the late-flowering period. Compared with the number of honeybees there were $1.31/0.25 = 5.30$ times as many native bees in the late-flowering period as in the mid-flowering period. The mid-points of the mid- and late-flowering periods were 8½ days apart, so in 1962 the ratio of native bees to honeybees showed more than a five-fold increase in little more than a week.

There are two possible explanations for the relative increase in the number of native bees in the late-flowering period; it might be due to the honeybees leaving *Leavenworthia* in favor of other plants as the number of *Leavenworthia* flowers decreases, or it might be due to an increase in the number of native bees.

The change in the ratio of native bees to honeybees can be explained as being due to the transfer of honeybees to other plants only if the percentage of honeybees working on *Leavenworthia* decreases four or five times more rapidly than the percentage of native bees working on *Leavenworthia.* This is possible, but unlikely. The populations studied in both periods include glade populations and cultivated populations. The largest field populations contained more than a thousand times the number of flowers in the smaller glade populations, and yet the relative increase in the number of native bees was similar in all populations. If the increase was due to the honeybees alone transferring to another crop one might expect the effect to be more pronounced on the smaller populations.

It seems much more likely that the change in the ratio of native bees to honeybees is due to an increase in the number of native bees foraging in the area. The available information on the seasonal activities of honeybees and native bees appears to support this conclusion.

Honeybees, unlike all other temperate Apoidea, do not hibernate during the winter, but remain intermittently active in the hives. Honeybees are foraging on *Leavenworthia* in suitable weather from the beginning of the flowering period (approximately March 15 in 1961 and March 20 in 1962 for *L. crassa* in the Massey-Lebanon district), but it is probable that the number of honeybees foraging increases somewhat as the *Leavenworthia* flowering season advances.

The native bees, on the other hand, hibernate during the winter, and emerge at some time during the warmer months of the year — the species differ widely in their dates of emergence and flight periods. There has been no detailed study of the flight periods of native bees in Alabama, but available information from studies elsewhere in the eastern United States (Michener and Rettenmeyer, 1956; Mitchell, 1960, 1962; Robertson, 1929) indicates that the number of bee species foraging increases greatly throughout the flowering period of *Leavenworthia*. All of the native bees collected have a wider distribution than the genus *Leavenworthia*, and must forage on other plants outside its range. Undoubtedly, these bee species forage on a variety of plants through a longer season than the relatively short flowering period of *Leavenworthia*.

The relative times of the flight periods of the native bees and the flowering of *Leavenworthia* suggest that the increase in the ratio of native bees to honeybees in the latter part of the flowering period of *Leavenworthia* is due to an increase in the number of native bee species foraging as the spring progresses, although a proportionately greater transfer of honeybees to other plant species cannot be ruled out as a contributing factor. It is unfortunate that I have no pollinator counts taken during the first half of the flowering season when the number of flowers is increasing. A similar increase in the ratio of native bees to honeybees during that time could only be interpreted as due to an increase in the number of native bees.

In addition the temperatures are lower earlier in the spring, and the daily flight periods are probably shorter at this time. Michener and Rettenmeyer (1956) observed that the daily period of flight of *Andrena erythronii* (possibly one of the species found on *Leavenworthia* — table 11) increases as the season becomes progressively warmer. Also, the average rainfall in the Tennessee Valley decreases as the spring progresses, so it seems likely that the percentage of days on which any flights are possible increases as the spring progresses. The combination of fewer native bees, fewer days suitable for flight, and shorter flight periods on suitable days earlier in the spring leaves no doubt that the earlier flowers are visited by fewer native bees than the later flowers. Consequently the flowers of those populations which are forced by the nature of the glade sites to cease flowering earlier in the season are on the average visited by fewer native bees than the flowers of populations on more favorable sites. Because of the association between self-compatibility and poor glade sites noted previously, this means that in general the flowers of self-compatible populations receive fewer native bees than the flowers of self-incompatible populations.

FACTORS AFFECTING THE EVOLUTION OF SELF-COMPATIBILITY IN L. CRASSA AND L. ALABAMICA

The nature of the selective forces responsible for the evolution of self-compatibility has been widely discussed in the century since the demonstration by Charles Darwin that cross-fertilization is generally advantageous to plants, and that many plant species have structural features which prevent or restrict self-fertilization. The earlier workers, including Darwin and Hermann Müller, generally attributed the evolution of self-compatibility to the need for an adequate seed set under conditions where cross-pollination was insufficient for this purpose. Since the rise of modern evolutionary theory many workers have replaced or supplemented this explanation with arguments based on differences in the genetical structures of cross-fertilized and self-fertilized species.

Genetical explanations for the evolution of self-compatibility are based on the theory of breeding systems developed principally by Darlington (*e.g.* 1939) and Mather (*e.g.* 1943a). These authors pointed out that the genetical structure of a population represents a compromise between the extent to which a population is adapted to its current environment, expressed as its immediate fitness, and its capacity to adapt to changes in the environment by producing new gene combinations, expressed as the flexibility of a population. Self-fertilization increases the degree of homozygosity in a population and therefore increases the number of genes which are expressed in a population; Mather consequently argued that a self-fertilizing plant can become more 'closely adapted' to its immediate environment. Self-fertilization also leads to a decrease in the genetic variability and therefore to a loss of flexibility. Consequently these authors believe that self-fertilizing plants achieve an increase in immediate fitness at the expense of a decreased flexibility.

Stebbins (1950, 1957) and others have extended this line of reasoning to suggest that self-compatibility may arise in species living in temporary, unstable habitats in response to the need for many well-adapted seeds under these conditions. In plants living under such conditions "a high premium is placed on a genetic system which favors opportunism and enables a favorable gene combination, once it has been achieved, to spread over a large number of genetically similar individuals" (Stebbins, 1950).

We may now examine the studies on the glade populations of *L. crassa* and *L. alabamica* and their pollinators to see which of the alternative hypotheses best explains the results.

Because of their physiographic position — at the base or on the lower slopes of limestone hills — the self-compatible glade populations of *L. crassa* and *L. alabamica* occupy drier glade sites than those occupied by most of the self-incompatible populations on the floor of the Moulton Valley. As a result, the self-compatible glade populations studied in 1962 were smaller and ceased flowering earlier in the spring than the self-incompatible glade populations. Moreover, the loss of self-incompatibility in several phyletic lines in *L. crassa* and *L. alabamica* probably occurred while the ancestors of the present self-compatible populations occupied glades similar to those of the self-compatible races today.

Estimates of the average number of bees visiting each flower in glade populations of various sizes in 1962 showed that the three smallest glade populations had many fewer bee visits than the six larger glade populations. The three smallest glade populations differed little in size, however, from two others which received many more bee visits to each flower. It may be that there is less chance of suitable nesting sites for bees existing near the smaller glades, rather than that the bees are less attracted to the smaller populations. But in either case the smaller size of the populations ancestral to the modern self-compatible races may have led to a diminished seed set through a lack of sufficient insect visitors.

The effect of the earlier flowering of glade populations in poor sites is clearer. Our knowledge of the seasonal foraging activity of the natural bee pollinators of *Leavenworthia,* and the relative increase in their numbers (compared with honey bees) in the second half of the flowering period of *Leavenworthia,* offers strong evidence that the earlier flowering populations receive relatively few bees to each flower; and even in the second half of the flowering period, when the bees are most numerous, each flower receives only a small number of visits (between 10 and 20 honeybee and native bee visits combined in most populations). An examination of the samples of plants from each of the undisturbed glade populations showed that up to 16 per cent of the flowers were not fertilized; and some of the flowers were undoubtedly self-pollinated without the aid of insects, even in the self-incompatible populations. This shows that there are indeed too few bees on those populations, or insufficiently frequent periods suitable for bees to forage, for all flowers to be pollinated by their activities. It seems likely therefore that the number of bee visits is inadequate to secure a full seed-set on the flowers produced earlier in the flowering season.

According to the above arguments, the loss of self-incompatibility in *L. crassa* and *L. alabamica* took place in small, earlier-flowering populations, the flowers of which received relatively few bee visits. The evolution of self-compatibility and of other characters associated with it increases the 'spontaneous' seed-set in the absence of insects, and may well have occurred in response to selection pressures favoring a fuller seed set. The results obtained in *Leavenworthia* thus agree well with the hypothesis that the evolution of self-compatibility and concomitant changes in *L. crassa* and *L. alabamica* have occurred as a response to the need for an adequate seed-set under conditions where cross-pollination was inadequate for this purpose.

On the other hand, there is some evidence that the supposed ability of self-fertilized plants to produce more closely adapted offspring has not been a factor in the evolution of self-compatibility in *L. crassa* and *L. alabamica.* I have no information on the relative growth and vigor of *Leavenworthia* plants resulting from self- and cross-pollinations, but in the only population tested (population 171 of the self-incompatible race c1) 653 out of 672 (97 per cent) seeds from cross-pollinations germinated, and only 39 out of 60 (65 per cent) seeds from self-pollinations germinated. The difference in percentages of germination was significant ($P<.01$).

Outcrossing is presumably advantageous in all self-incompatible races; otherwise, as Mather (1943b) pointed out, *any* suitable mutant conferring self-compatibility would increase in a population, since it would succeed in self-pollinations as well as in cross-pollinations. An increase in inbreeding in an outbreeding species will thus inevitably lead to inbreeding depression. It can hardly be argued, therefore, that the increase in inbreeding accompanying the *actual loss* of self-incompatibility produces an immediate gain in the average fitness of a population.

The evolution of self-compatibility in *Leavenworthia* must have had another adverse effect on seed production. It was mentioned above that in both self-incompatible and self-compatible populations, on the average, fewer seeds are produced in each silique after self-pollination than after cross-pollination. The increase in inbreeding accompanying the evolution of self-compatibility would therefore be expected to decrease the average number of seeds produced in each silique, and in this respect would decrease the fitness of a population.

The lower number of seeds per silique after self-pollination and the presence of heterosis in the self-incompatible races suggest that the evolution of self-compatibility in *Leavenworthia* can only be due to a selective advantage acting prior to fertilization that is, a greater percentage of flowers being pollinated. This advantage appears to have arisen through the paucity of bees on smaller, earlier flowering populations occupying drier glades, and must have been sufficient to compensate for decreases in the number and quality of seeds resulting from each self-pollination.

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A TAXONOMIC REVISION OF CREMOLOBUS (CRUCIFERAE)

KULDIP R. KHANNA AND REED C. ROLLINS

Cremolobus, which literally means "the pendant lobes" and refers to the hanging valves of the silique, is a very distinctive genus of the *Cruciferae*. It was separated from *Biscutella* by De Candolle (1821) because of the thick pyramidal style, pendulous valves that are not adnate along their entire length and stipitate siliques. Three species were originally placed in *Cremolobus* by De Candolle. Since then a total of 17 species has been ascribed to the genus at one time or another. More recently, *Cremolobus* has received treatments by Schulz (1936) and by Macbride (1938). The latter author discussed the Peruvian species in some detail and dealt with nearly all of the species included in the present treatment. The exceptions were those whose occurrence in Peru was doubtful. The criteria used by these and earlier authors have been critically examined by us. Our study has been based on a larger number of collections than was previously available, making possible the careful comparison of various transitional types over a wide geographic range. As a result, we have found it prudent to place a number of previously recognized species together, particularly under *C. chilensis*.

Each of two species of *Cremolobus*, *C. rhomboideus* and *C. stenophyllus*, has previously been raised to generic rank. Muschler (1908) erected the monotypic genus *Urbanodoxa*, basing it on *C. rhomboideus*. Later Schulz (1933) described *Loxoptera*, ascribing the single species *C. stenophyllus* to it. The characters presumed to separate these species as genera distinct from *Cremolobus*, though definite in occurrence, are either variable intraspecifically or show sporadic occurrence in other species of *Cremolobus*. Hence, it is unrealistic to maintain *Urbanodoxa* and *Loxoptera* as monotypic genera apart from *Cremolobus*. However, a discussion of each case is given individually under the species concerned.

GENERIC RELATIONSHIPS

Despite the early association of species of *Cremolobus* with *Biscutella*, it is clear that the more significant relationship is in the direction of *Menonvillea.* An extreme reduction of the replum and consequently of the septum, the frequent occurrence of a distinct gynophore, a strong tendency for the individual valves of the silique to become almost completely closed around the single seed and the usual presence of wings or their remnants on the valves are all features common to *Cremolobus* and *Menonvillea.* However, the orientation of the valves with respect to the replum is quite the opposite in the two genera.

The placing of *Cremolobus* and *Menonvillea* together accords with the treatment of Schulz (1936) where they are admitted to the tribe *Cremolobeae.* That author subdivided the *Cremolobeae* into subtribe *Cremolobinae* and subtribe *Menonvilleinae,* each with three genera. However, in our studies including previous work (Rollins, 1955), only two genera are recognized in place of six. Unlike the Schulz presentation, we would neither subdivide the *Cremolobeae* nor place genera such as *Biscutella* and *Dithyrea* completely outside of the tribe including *Cremolobus* and *Menonvillea.*

GENERAL CHARACTERISTICS OF THE GENUS

A majority of the species of *Cremolobus* is centered in Peru, which is also the area of greatest diversity. However, the genus as a whole has a much wider distribution in the Andes of South America than Peru alone. It extends a few degrees above the Equator and is reported as far south as Coquimbo in Chile, although this record is in doubt. *Cremolobus* is mostly a genus of high altitudes, the majority of the members growing above 6,000 feet and some reaching 13,000 - 14,000 feet. However, the plants of some species occur at lower elevations as well. Some collections of *C. chilensis* have been made from as low as 1,000 - 1,500 feet and *C. stenophyllus* and a variety of *C. bolivianus* are known to occur at an intermediate range of 4,000 - 5,000 feet.

The genus is represented by tiny herbs barely 3 cm. tall at one extreme and on the other by shrubby types like *C. peruvianus* that are reported to grow as tall as 5 meters. With the exceptions of *C. peruvianus* and the imperfectly known *C. suffruticosus* and *C. subscandens,* the rest of the species are strongly herbaceous, only occasionally having a tendency towards suffrutescence at the very base.

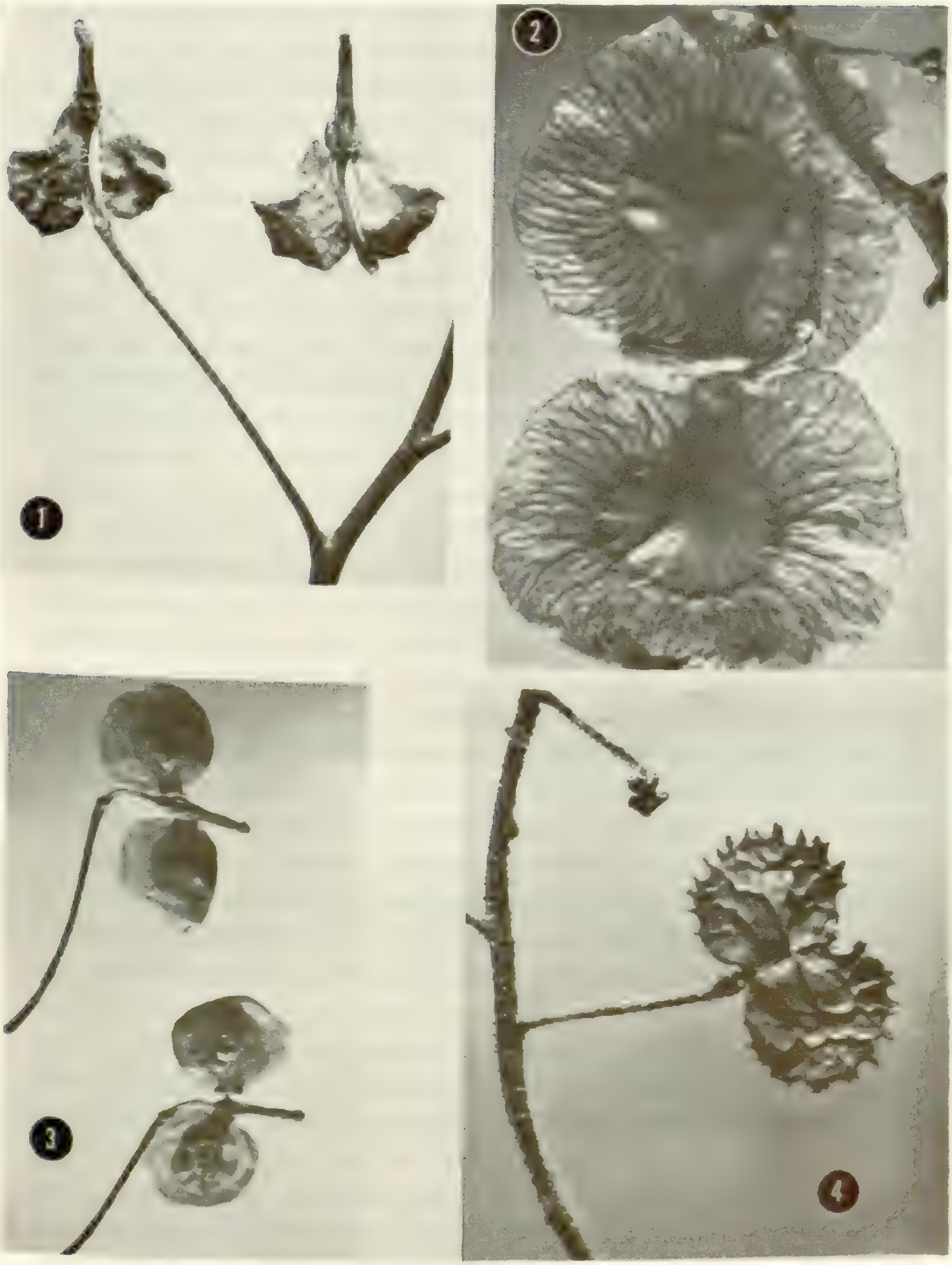

FIG. 1-4. Siliques of *Cremolobus*. FIG. 1. Siliques of *C. rhomboideus*. FIG. 2. Siliques of *C. peruvianus*. FIG. 3. Siliques of *C. stenophyllus*. FIG. 4. Siliques of *C. bolivianus*.

The stems are ordinarily profusely branched. In some specimens of *C. chilensis*, the branching is noticeably profuse right from the base. The stems may be solid or fistular and range from less than 1 mm. to 8 mm. in diameter as found in some branches of *C. peruvianus.* The thickness of the stem must be much greater in this species than in any other, although no complete specimens have been observed to fully authenticate such a statement. The stems may be rounded or somewhat angular, with longitudinal furrows running along the entire length, as may be seen in some herbaceous types. The stem pubescence, like the pubescence of the other parts of the plant, is a very variable character in this genus, although the pubescence of each part is independent of every other. The differences in stem pubescence are a very noticeable feature of *C. peruvianus, C. chilensis* and *C. bolivianus.* The trichomes are dendritic, consisting of 6 - 8 rays or branches in *C. peruvianus* and *C. bolivianus,* while in the other species, when present, they are simple, unbranched and with flattened bases.

The leaves are opposite in two species, *C. bolivianus* and *C. subscandens,* and alternate in the rest. Sometimes in the alternate leaved species, the leaves are opposite or subopposite. They vary in shape from linear-lanceolate to ovate-oblong or ovate-rhomboidal. Their size ranges from those present on the smallest plants of *C. chilensis,* where they are not more than 0.5 cm. long and 0.4 cm. wide, to those of the large shrubby plants of *C. peruvianus,* where they are up to 12 cm. long and 4.5 cm. in width. In the latter, the leaves are quite hard and leathery in texture, this being the only species of the genus with this characteristic strongly developed. The leaves are usually markedly petiolate, the petiole being well developed in most species except in *C. chilensis,* where the leaves are sometimes subsessile. The margin is somewhat serrate in all species, becoming dentate to variously pinnatifid in some plants of *C. chilensis.* The leaves may be shallowly lobed, with the lobes close together, or deeply lobed with the lobes remote from each other. The lobes themselves may be entire or serrate, and are usually acute. Sometimes there is a tendency toward a bipinnatifid condition in *C. chilensis.* The leaves of *C. peruvianus* and *C. bolivianus* are the most strongly pubescent of the genus, although here, as in the other species, some specimens were observed to lack pubescence completely. The trichomes, like those of the stem in these species, are stellate and dendritic and are situated mostly on the lower surfaces of the leaves, especially along the veins. In the other species of the genus, the leaves are only sparsely pubescent with minute trichomes or they are glabrous. In these cases, the trichomes are simple, with bases flattened to a varying degree, and are scattered on the leaf surface. Here again, the pubescence is almost wholly confined to the lower surfaces. The leaves of *C. stenophyllus* and *C. suffruticosus* are completely glabrous.

The flowers are borne in elongated or semi-corymbose racemes. The size of the flower, as reflected by the petal length, ranges from 2 mm. to 5 mm. and in several cases considerable within-species variation was observed in the flower size, particularly in *C. chilensis*. The flower color in the genus as a whole ranges from white to creamy or sulphur yellow becoming somewhat darker on drying in *C. peruvianus*. The structure of the flower is that of a typical crucifer and is quite uniform for the entire genus. The sepals are green or yellowish green in color, boat-shaped and hyaline-margined. The venation is sparse and is present only in the central non-hyaline region. The sepals are usually glabrous but may sometimes possess a few trichomes on the outer basal portion in *C. peruvianus*. They are in two pairs which are differentiated from each other. The outer pair consists of relatively narrow sepals arising from narrower bases than those of the inner pair. The members of the outer pair are also less deeply keeled than those of the inner. The petals are about one and half times longer than the sepals but rarely the sepals and petals are subequal. The petals are entire to wavy margined and are spatulate to distinctly clawed. The nectaries are inconspicuous to well developed. The stamens are tetradynamous with filaments gradually and not abruptly flattened at the base. The anthers are sagittate and dehisce by longitudinal slits on the inner side. The ovary in most species is supported on a distinct gynophore. The gynophore is rudimentary in *C. bolivianus* and *C. subscandens*. The ovary is initially bilobed and flattened at right angles to the septum. It continues to develop in the same pattern, ultimately becoming the characteristic fruit of *Cremolobus*. The styles are long, somewhat flattened to triangular, except in *C. peruvianus* (fig. 2) where they are peg shaped. The stigma is capitate, usually exceeding the upper portion of the style in diameter. In *C. bolivianus* (fig. 4) and *C. subscandens,* like the gynophore, the style is rudimentary and is completely covered over by the capitate stigma at maturity.

The fruits are borne on pedicels that may be pubescent or glabrous and vary considerably in length. They may be horizontal, sigmoid or ascending. In *C. subscandens*, the pedicels are nearly erect, paralleling the axis of the infructescence. In *C. suffruticosus*, they are very distinctive, being the longest in the genus, i.e., up to 2.5 cm. long. The pedicels in this species are also more flattened in contrast to the cylindrical ones of the other species. The shape of the fruit is distinctive because the valves of the silique not only hang from the replum but are also flattened in a plane that is perpendicular to the face of the replum. Exceptions to the pendant position are found in *C. subscandens*, *C. bolivianus* and *C. peruvianus*, where the valves are horizontally oriented to the main axis of the replum. The presence of a gynophore is also a very characteristic feature of the genus, even though it is very much abbreviated in *C. bolivianus* and *C. subscandens*. The development of the gynophore in most species is very striking, being almost as long as the style (cf. fig. 1, 3 & 8). However, it is sometimes considerably shorter than the style in *C. suffruticosus*. The valves of the fruits are laterally winged or wingless, but the extent of winging varies to some extent. *C. bolivianus*, *C. subscandens* and *C. rhomboideus* have completely wingless valves. The most variable species with respect to this character is *C. chilensis* (fig. 5-10). Here, the development of the wings takes place to a varying degree. The valves of the other species have well developed wings, the largest of which are found in *C. peruvianus*. The wings are veined in this species (fig. 2), a character not present elsewhere in the genus. The wings are translucent in *C. stenophyllus* (fig. 3) where, in addition to the principal wings, the valves also have minor cross wings rolled inward, both above and below. The surfaces of the valves are smooth in *C. peruvianus* and in some individuals of *C. chilensis*. They are radially wrinkled and thick walled in *C. rhomboideus* (fig. 1) and reticulate in *C. bolivianus* (fig. 4) and *C. subscandens*. The valve surfaces in some plants of *C. chilensis* have various sizes of simple trichomes (fig. 6, 9 & 10). The margin of the valves, when not winged, ranges from simple to dentate.

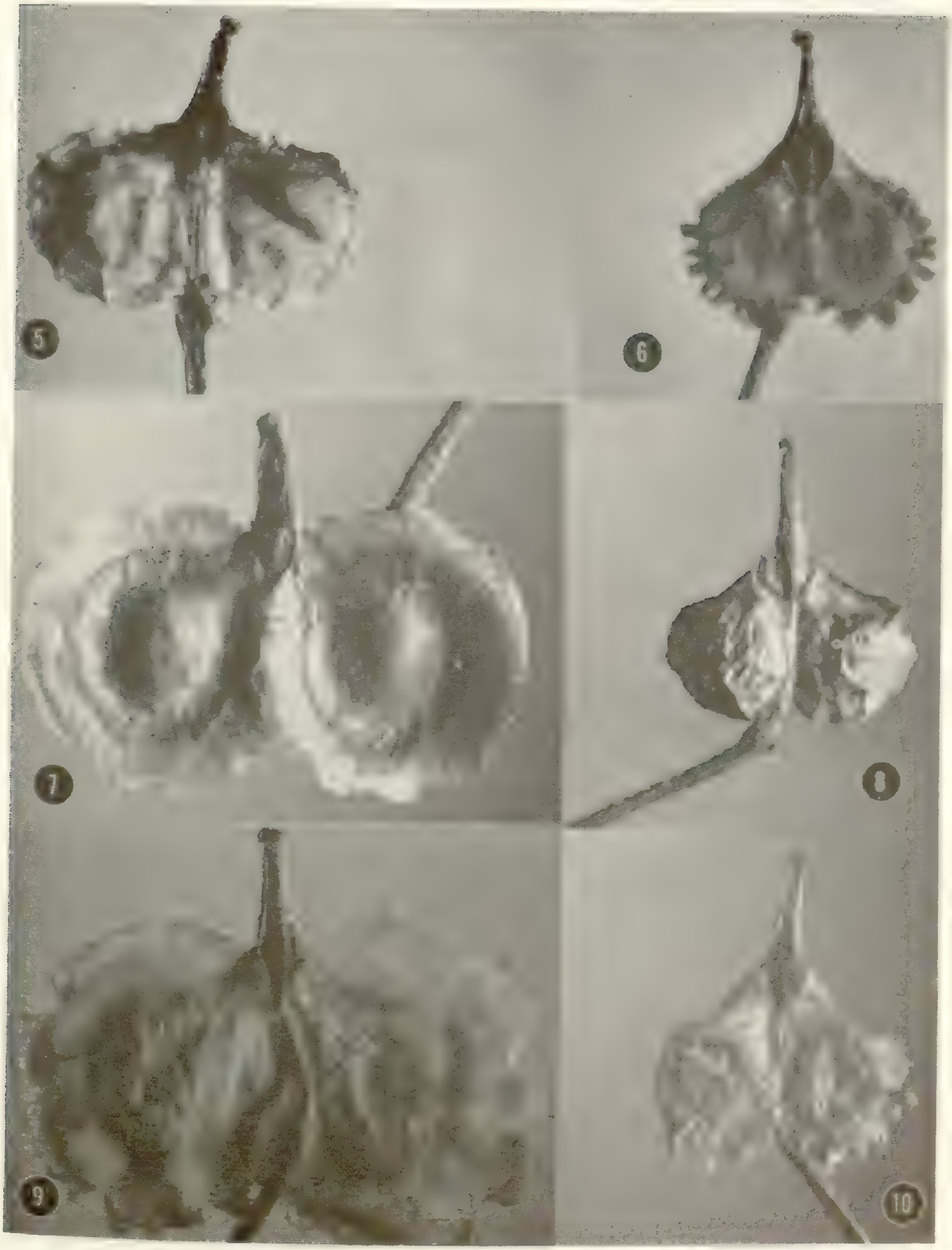

FIG. 5 - 10. Siliques of *Cremolobus chilensis* showing range of variation within the species. FIG. 5. Glabrous silique with weak reticulation and abbreviated wings. FIG. 6. Pubescent silique with crenate abbreviated wings. FIG. 7. Glabrous silique with well developed, nearly entire wings. FIG. 8. Glabrous, wingless and slightly reticulate silique. FIG. 9. Densely pubescent silique with well developed somewhat crenate wings. FIG. 10. Pubescent and nearly wingless silique with somewhat elongated valves.

The seeds are orbicular to suborbicular, flattened and brown in color. They are attached by either a long or a short funicle. The cotyledons are always accumbent.

ACKNOWLEDGEMENTS

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TAXONOMIC TREATMENT

CREMOLOBUS DC., Systema 2: 418. 1821

Annual or perennial; small herbs to undershrubs or shrubs; stems unbranched to profusely branched, often from the base; leaves alternate to opposite, sessile or petiolate, entire to deeply pinnatifid, glabrous or pubescent with simple flat or stellate trichomes; inflorescences racemose, compact to greatly elongated, flowers pedicellate, pedicels glabrous or pubescent on the upper or on both the upper and the lower sides; sepals green or yellowish green, pouch-like at the base, hyaline margined, sparsely veined in the central non-hyaline region, inner and outer pair differentiated from each other; petals white to cream, mostly clawed, entire or with a wavy margin; nectaries inconspicuous to well developed; stamens tetradynamous; style absent or short and peg shaped to elongated and triangular; stigma usually distinct from the style; gynophore well developed or sometimes obsolete; replum rhomboidal or elongated with two laterally attached valves; valves triangular, suborbicular to orbicular, smooth to reticulate, glabrous to pubescent, winged to wingless, rarely with cross wings, each valve enclosing a single seed; seeds orbicular; cotyledons accumbent.

KEY TO THE SPECIES

A. Leaves opposite; silique reticulately ridged, sessile, wingless; stigmas sessile.
  B. Plants densely pubescent with conspicuous trichomes; leaves ovate-lanceolate to linear-lanceolate, lower about 9 cm. long and 3 cm. wide; pedicels mostly horizontal .... 1. *C. bolivianus.*
  B. Plants sparsely pubescent with minute trichomes to glabrous leaves ovate rhomboidal, 4-5 cm. long and 2-3 cm. wide; pedicels mostly ascending to erect, often nearly paralleling the stem. .... 2. *C. subscandens.*
A. Leaves alternate; siliques not reticulate, distinct gynophore present, wings well developed to absent; styles conspicuous.

C. Plants perennial, suffrutescent, undershrubs or vinelike in habit.
  D. Plants pubescent at least in the upper part; pedicels about 1 cm. or less long; valves 10 mm. across, horizontal; styles short and thick .... 3. *C. peruvianus.*
  D. Plants glabrous; pedicels 1-2.5 cm. long; valves 2-3 mm. across, pendant; styles thin and elongated 4. *C. suffruticosus.*
C. Plants annual, herbaceous throughout.
  E. Valves with secondary wings at right angles to the principal wings; margins of the principal wings rolled, thin and translucent .... 6. *C. stenophyllus.*
  E. Valves without secondary wings; margins of the wings not rolled, mostly thin but opaque.
    F. Plants up to 1.25 m. tall: pedicels up to 2 cm. long; valves triangular, turgid, hard and woody in texture, completely wingless, stigma not markedly different from the style in diameter .... 7. *C. rhomboideus.*
    F. Plants 3-35 cm. tall; pedicels not more than 1 cm. long; valves triangular to orbicular, mostly flat or lens shaped in the center, thin and papery, winged to wingless; stigma distinct .... 5. *C. chilensis.*

1. **Cremolobus bolivianus** Britt. Bull. Torrey Club 16:17. 1889

Perennial; stems branched, densely pubescent with simple or dendritically branched trichomes; leaves opposite, shortly but distinctly petiolate, ovate-lanceolate to linear-lanceolate, lower 9 cm. long and 3 cm. wide, minutely and distantly toothed, acute to acuminate, densely pubescent on the lower surface especially along the veins, less so on the upper surface, trichomes of the lower surface much larger than those of the upper; inflorescences lax, pedicels mostly horizontal, 5-7 mm. long, pubescent; sepals green, oblong, obtuse, 2 mm. long, margin hyaline, well developed toward apex, sepals differentiated into an outer and an inner pair; petals whitish to cream, darker when dry, spatulate, 2.5 mm. long, entire, wavy in the region of the blade; nectaries 4, prominent; paired stamens 1.5 mm. long, filaments narrowed toward the point of attachment with the anthers, anthers sagittate; gynophore nearly obsolete; style very short, inconspicuous when mature, nearly covered over by the bifid, capitate stigma; replum elongate, valve attachment to replum extending nearly the length of the valve; valves somewhat fused with each other at the point of attachment, 4 mm. across, horizontal, reticulate, wingless, margin strongly dentate, sometimes pubescent; seeds about 1 mm. across, funicle very short; cotyledons accumbent. Fig. 4.

BOLIVIA: Unduavi, 8,000 ft., October, 1885, *Rusby 1816* (NY, Type; GH, US, isotypes); in the vicinity of Ananea, Parjchani (Prov. Larecaja), June, 1860 *Mandon 905 bis* (G).

Opposite leaves and opposite branching are strongly fixed features of *C. bolivianus* and *C. subscandens* and the two species are obviously very closely related if not variants of the same species. The pubescence is definite and pervasive on the specimens we have seen of *C. bolivianus,* while it consists of minute flattish trichomes scattered along the veins of the under surfaces of the leaves or is completely absent in *C. subscandens.* Other minor differences, as indicated in the key and in the descriptions, tend to correlate to give some substance to the evidence for the recognition of two taxa. However, more adequate specimens and field work are needed to provide the data for a more reliable interpretation than we can give at present. If both taxa had not been described at the specific level, we would be inclined to consider one of them as a subspecies of the other.

2. **Cremolobus subscandens** Kuntze, Rev. Gen. 3 pt. 2:4. 1898

Perennial; stems branched, suffrutescent, sparsely pubescent with short simple trichomes, branching opposite, at least above; leaves opposite, ovate to ovate-rhomboidal, 4-5 cm. long and 3-5 cm. wide, serrate, acute, veins sparsely and minutely pubescent on the lower side, texture stiff; pedicels not exceeding 0.5 cm. in length, ascending to nearly erect, glabrous; sepals green, outer and inner pairs different in width and point of attachment, ca. 2 mm. long; petals white, spatulate, 2.5 - 3 mm. long; nectaries poorly developed; stamens distinctly short and long, anthers elongate, sagittate; gynophore absent; style very short, completely covered over by capitate stigma at maturity; replum elongated, valve attachment extending nearly along the entire length of the valve, valves horizontal with respect to replum, 4 mm. across, surface reticulate, wingless, margin dentate, sinus between the valves broad and smooth; seeds dark brown, 1-2 mm. across, funicles not conspicuous; cotyledons accumbent.

BOLIVIA: Rio Funtas, 1800 m., 13-20 April, 1892, *Kuntze* (NY, type; photo of isotype at B; F, GH); Cochabamba, Incachaca, 2200 m., October 14, 1921, *Steinbach 5885* (F, GH, LIL, US); near Yungas, 4,000 ft., 1885, *Rusby 1820* (GH, NY, US). ARGENTINA: Ledesma, (Prov. Jujuy), October 2, 1906, *Dinelli 5108* (GH, LIL).

From limited herbarium material, it is difficult to gain any real conception of what the plants of this species are like. The name Kuntze applied suggests that growing plants are weak stemmed and at least dependent on other plants for support, if not actually climbing in habit. The specimens are in accord with this idea. Not a single one has the basal portion of a plant present and the material of each collection appears to have been taken as ultimate flowering or fruiting branches. We have no evidence as to height of the plants or distance of the remotest branches from the ground.

Not one of the seven sheets we have for study shows more than one or two developed fruits per inflorescence branch even when the number of pedicels with an abortive ovary is 20 or more. This suggests that pollination is relatively inefficient, at least in areas where specimens have been collected. A general remoteness of one plant from another, either spatially or by interspersion of other plants, may also be inferred as a possibility.

Both *C. subscandens* and *C. bolivianus*, if they are in fact distinct species, would be rewarding for further study and collecting. True climbers are certainly rare if not absent in the Cruciferae, but these are the best candidates we know of to possess the climbing feature.

3. **Cremolobus peruvianus** (Lam.) DC., Systema **2**: 419. 1821

Biscutella peruviana Lam., Encycl. Méth. 3: 620. 1791.
Cremolobus pubescens Hook., Icon. Pl. t 81. 1837.

Perennial; stems woody, branched, glabrescent and smooth below, pubescent in the upper parts with 6-10-rayed stellate trichomes; leaves alternate, petiolate, ovate-lanceolate, lower large, up to 12 cm. long and 4.5 cm. wide, upper much shorter, 2.5 cm. long and 1-3 cm. wide, serrate, acute, rarely acuminate or emarginate, upper surface deep green, sparsely pubescent, lower surface pale green and more profusely pubescent, leaves often completely glabrous, veins prominent on the lower surface, petioles 5-9 mm. long; pedicels pubescent, up to 1 cm. long when mature, horizontal to slightly curved upwards; sepals greenish, glabrous, or rarely with a few trichomes on the lower portion, obovate, 3-4 mm. long, margin hyaline, the veins confined to the central region, not entering the hyaline portion, keeled, outer pair linear and less deeply keeled as compared to the inner, which is broader and more pouch-like; petals cream to sulphur yellow, somewhat orange colored when dry, linear obovate, distinctly clawed, 5-7 mm. long, blade margin wavy or entire; stamens distinctly long and short, the longer ones 4 mm. long and the shorter ones 2 mm. long, anthers sagittate, introrse; nectaries 4, prominent; gynoecium raised on a smooth gynophore, style short, thick, about the same diameter as the replum area below it, smooth when young but ridged in the mature fruit; stigma capitate, covering the style like a triangular cap, depressed in the center, reddish in color, nearly of the same diameter as the style when young; valves attached horizontally on the replum, orbicular, glabrous, wings well developed, reticulately veined, entire; seeds attached by a thin funicle about 1 mm. long, brownish to dark red, suborbicular, 2-2.5 mm. long, surface marked by fine reticulations, one seed in each locule; cotyledons accumbent. Fig. 2.

Cremolobus pubescens, as described and illustrated by Hooker, is similar to *C. peruvianus* in all the characters given, such as the suffrutescent habit, the pubescence, the panicled inflorescence, and particularly the shape of the fruit and style, which are very characteristic features of *C. peruvianus*. The only noticeable difference from *C. peruvianus* is in the illustration of the flower where the sepals and petals look nearly equal. Probably the material examined by Hooker was young both as to flowers and fruits. In both figures where fruits are represented, younger material appears to have been the basis for the illustration and the same is true of the flower, which does not seem to have opened fully. In such a stage of development, the relative size of the sepals and petals is likely to be misjudged, since the full size of the petals is manifested only when the flower is fully open.

DISTRIBUTION: Colombia, Ecuador and Peru. De Candolle cited a Dombey specimen from Chile in his Systema (1821) but in an earlier treatment of *C. peruvianus* (1811), it was given as Peru. Since we have no subsequent evidence that the species extends to Chile, we assume the citation in the Systema is in error.

COLOMBIA: Cauca. 'San Jose', San Antonio, altitude 2100-2500 m., July 1, 1922, *Pennell 7630* (GH); Hoya del rio Tambito, Mt. Munchique, Occidental Cordillera, 2000-2500 m., July 16, 1939, *Arbelaez and Cuatrecasas 6209* (F, US); near Puenta de Tierra, 2200 m., September 13, 1944, *Core 1249* (WVA). ECUADOR. Corazon, Mission Scientifique de *Ed. Andre K160* (F, GH, NY, US); Mojanda, 1906, *Herb. Lehmannianum 5400* (F, GH, NY, US); Malchingui to Pomasqui, Pichincha, 3000-3600 m., August 13, 1923, *Hitchcock 20870* (US); Mindo, June 26, 1876, Mission Scientifique de *Ed. Andre K161* (NY); San Miguel on margin of paramo between Atuntiaqui and Hacienda Pinon (Prov. Imbabura), 11,300 ft., June 20, 1944, *Wiggins 10,334* (GH); western side of Pichincha, *Jameson* (G, GH, NY, US); Cinto Santuario, S.E. de Lloa (Prov. Pichincha), 3200 m., July 28, 1927 *Firmin 153* (US); Quito, 1848, *Jameson* (G); Andes of Quito, 1859, *Jameson* (G, GH, NY); Quito-Popayan-Bogota, 1843, *Hertweg 886* (G); Supra rio Cristal, Occidental Cordillera, July 10, 1876, Mission Scientifique de *Ed. Andre 4005* (F, GH, NY, US); Nudo de Portete, pass between head waters of the rios Tarqui (Atlantic) and Giron (Pacific) (Prov. Azuay), about 9000 ft., March 10, 1945, *Camp E-2176* (NY); 1-8 km., north of the village of Servilla de Oro, Eastern Cordillera, (Prov. Azuay), 8000-9000 ft., July 28-August 12, 1945, *Camp E-4351* (GH); Andes, 1857-1859, *Spruce 5019, 5506, 6049* (F, G, GH, NY); 1860, *Fraser* (G); Tropical South America, 1862, *Fraser* (BM). PERU: *Jussieu* (frag. of type, F); 1827, *Pavon* (F, G); *Ruiz and Pavon*

1778-1788 (F); Rio Masamerich (Dept. Junin), 2200-2300 m., 1909-1914, *Weberbauer 6673* (F, GH, NY); upper slopes and summit of Cerros de Calla-Calle, near kms. 403-407 of Balsas-Leimebamba road, Prov. Chachapoyas (Dept. Amazonas), Aug. 18, 1962, *Wurdack 1695* (US).

Cremolobus peruvianus is of considerable interest because of the vine-like growth habit and the divided paniculate raceme with the subdivisions most frequently in the axils of bracts. In turn, the branches bearing the inflorescences are in the axils of leaves. The stem is definitely woody. The habit of growth, the inflorescence form and the woody nature of the stem are all unusual characteristics for the family Cruciferae. From specimens alone, it is difficult to reconstruct an exact description of the whole plant because the basal portions are not included. Notes on a few of the labels indicate the species may be either vine-like or shrubby, with stems up to 5 meters in length. On a number of specimens, the leaves are all oriented in one direction, indicating that the stem on which they were borne was reclining.

Aside from the habit of growth, there are other deviating characteristics evident in the specimens the taxonomic significance of which cannot be completely assessed from the specimens alone. For example, among the collections here referred to *C. peruvianus*, some specimens have completely glabrous leaves, in others the leaves are sparsely pubescent with either simple trichomes or with dendritic trichomes and in one collection (Camp E-4351) the lower leaf-surfaces are densely pubescent with short simple trichomes. It is possible that these differences have some taxonomic significance but we have not been able to find any correlation with other distinctions. Until special studies can be made to carefully elaborate on the nature of the growing plants and the significance of such deviations as we have pointed out, we have felt impelled to provide a conservative treatment that emphasizes the similarities we can assess rather than the differences.

It should be pointed out that the type of *C. peruvianus* has glabrous leaves.

4. **Cremolobus suffruticosus** DC., Systema 2: 419. 1837

Biscutella suffruticosa DC., Ann. Mus. Hist. Nat. Paris 18: 296, tab. V. 1811.

Perennial shrubs or under shrubs, height unknown; stems alternate, woody, glabrous; lower leaves unknown, upper ones alternate, petiolate, ovate-oblong, 2.5 cm. long, 0.6 cm. wide, entire or minutely to strongly serrate in the distal portion, glabrous both on the upper and lower surfaces, petiole up to 5 mm. long; pedicels comparatively long, slender, up to 2.5 cm. when mature, sigmoid to irregularly directed upwards, glabrous; sepals green, broadly ovate, obtuse, 3 mm. long, hyaline margined, boat shaped, differentiated into an outer and an inner pair, upper part of outer pair with large flat trichomes; petals whitish, somewhat darker when dry, 5-7 mm. long, margin in the region of the blade wavy; stamens tetradynamous, filaments narrowed towards the point of anther attachment, anthers elongate, sagittate, introrse; gynoecium raised on a short thin gynophore; style short and thick when young, thin and elongate when mature, stigma capitate; valves pendant with respect to replum, more or less orbicular, wings present, glabrous; seeds not observed.

As compared to *C. peruvianus*, the flowers of *C. suffruticosus* are considerably larger, and both pedicels and styles are more than twice as long. The two species should not be easily confused because of these striking differences but it is clear that Macbride (1938) did not properly distinguish between them.

C. suffruticosus is evidently quite rare. To our knowledge, it has not been collected outside of Peru, even though it has been attributed in the literature to both Chile and Ecuador.

The above description is based on rather poor specimens. We have seen only a fragment of the original material collected by Dombey and not the Lagasca specimen. However, the plate accompanying De Candolle's proposal of the species is very helpful in interpreting the few available specimens.

PERU: *Dombey* (frag. of type, F); Chechin, *Dombey* (F); 1827, *Pavon* (F, G); vicinity of Baños, Wilkes Expl. Expedition 1838-1842 (US); Mahuay, Prov. Bolognesi, Dept. Ancash, Peru, on May 22, 1954. *Cerrate 2216* (GH).

5. **Cremolobus chilensis** DC., Systema 2:419. 1821

Biscutella Chilensis DC., Ann. Mus. Hist. Nat. Paris 18: 297, tab. VI, 1811.
B. cuneata Lagasca, Gen. Spec. Pl. Nov. 20. 1816.
Cremolobus sinuatus Hook., Icon. Pl. t 99. 1837.
C. pinnatifidus Hook., Icon. Pl. t 100. 1837.
C. aphanopteris Gray, Bot. U.S. Expl. Exp. 55. 1854.
C. pinnatifidus var. *integrifolius* Gray, Bot. U.S. Expl. Exp. 56. 1854.
C. parviflorus Wedd., Ann. Sci. Nat. Ser. 5. 1: 283. 1864.
C. humilis Musch., Engl. Bot. Jahrb. 40: 269. 1908.

C. Weberbaueri Musch., Engl. Bot. Jahrb. 40: 170. 1908.
C. Paysonii Schulz in Macb. Field Mus. Pub. Bot. 8: 80. 1930.
C. Benoistii Macbr. Field Mus. Pub. Bot. 13 (2): 941. 1938

Annual herbs; 3-35 cm. tall; tap roots mostly unbranched; stems profusely branched from the base or in the upper portion, angular, sometimes pubescent in the younger parts; leaves alternate, the lower ones occasionally opposite, subsessile to petiolate, petiole up to 1 cm. long, blade linear-ovate or rhomboidal, serrate to deeply pinnatifid, leaves including petiole 0.5 cm. to 5.0 cm. long, 0.4 cm. to 1.5 cm. wide, glabrous to minutely pubescent on both the upper and lower side; pedicels up to 1 cm. long when mature, horizontal, sigmoid or divaricately ascending, glabrous or minutely pubescent on the upper side with flat pointed trichomes; sepals greenish, hyaline margined, veined only in the central region, 2 mm. long, outer pair narrow and with a narrow base, inner pair broader with a broader base and deeper keel; petals white, 2.5-3 mm. long, spatulate to distinctly clawed, entire or wavy in the upper region; nectaries well developed; stamens tetradynamous, distinctly long and short, filaments flattened at the base, anthers heart shaped or slightly more elongate, sagittate, introrse; gynoecium raised on a thin gynophore which may be about as long as the style when mature or slightly longer; style conical, broadening at the base into expanded replum; stigma capitate; siliques bipartite; valves pendant, attachment to replum constricted compared to valve diameter, valves triangular to suborbicular or orbicular, 1.5-4 mm. across, flat or sometimes sunken around the seed, occasionally with prominent radial folds, winged or wingless, wings entire to deeply fringed, smooth to rough in texture, glabrous to variously pubescent, creamy to brown in color; seeds single in each valve, attached by a short white funicle, yellowish to dark brown in color, suborbicular; cotyledons accumbent. Fig. 5-10.

Cremolobus chilensis is a highly polymorphic species and has the widest distributional range in the genus. The largest number of collections are from Peru, while only a few collections have been made from adjoining regions of Bolivia, Argentina and Chile. This species ranges in altitude from 1,300-10,000 feet. As might be expected in a plant of such diverse altitudinal and climatic zones, there exists a considerable difference in time of flowering and fruiting (February to September). This species is very variable with respect to size, branching of the stem and the characteristics of the leaves and fruits. These characters seem to be independently determined genetically. In most cases, they are uncorrelated, making it hard to study any one of them consistently with the rest. Any one of these characters might have been of specific importance had its development been associated with an isolating mechanism of some sort. To be effective, such an isolating mechanism controlling the flow of genes that determine a particular character would have to coincide with ecological or geographical niches of importance to the specific populations. But the occurrence of a whole array of transitional types over the entire range of the species, points in another direction. In the following, the characters which formed the basis for a number of proposed species given in the synonmy list, are discussed in some detail.

The size of the plant varies from 4-35 cm. in height. There does not appear to be any definite correlation between the size and other characteristics of specific rank or even with the geographic distribution of the species. However, of the few collections available from southern Peru, Bolivia, and Argentina, most of them had much smaller sized plants than are usually present in the more abundant collections farther north. These small plants may represent only the chance factor involved in making the collections or possibly they grew under the less favorable circumstances than the larger specimens. Size in annual plants is known to be extremely variable and sensitively reflects the quality of the environment. We suspect that this is the case in *C. chilensis*. Since size as a character may be both environmentally and polygenically determined, it cannot, by itself, be assigned a high degree of taxonomic importance.

The leaf characters are similarly variable. The leaf size, which is to some extent correlated with the height and general habit of the plant, ranges from 0.5-5.0 cm. and is of little specific value. The authors describing the species given in the synonymy list described the leaf shape variously as ovate, oblong, ovate-oblong, spatulate, subrhomboidal, lanceolate, oblanceolate, elliptic, etc. By examining the available collections, we cannot escape the conclusion that these leaf shapes are closely interconnected and any one of them is by no means a specific criterion. Similarly the nature of the leaf margin is a very flexible character, sometimes observably so in the same plant. The lower leaves may be entire when the upper are pinnatifid. More often the variability of this character is observed in the members of the same population where some plants have entire or serrate leaves and the others have deeply pinnatifid ones. This may be neatly observed in the collection, *Stork, 11441* (GH).

The fruit characters have been greatly relied upon as the key features for distinguishing the purportedly separable species whose names are listed above in the synonymy. These include size of fruit, shape of the valves (triangular to suborbicular to orbicular), development or the lack of development of the wings, margin of the wings (entire or variously lobed), and pubescence (its presence or absence or unequal development). These characters (cf. fig. 5-10) may vary from one plant to another in the same population and their expression is sometimes dependent upon other features as well. The size of the fruit, for instance, is often related to the vigor of the plant or to the development of the wings. The ultimate shape of the fruit is also considerably influenced both by the shape of the valves and development of the wings. The dentation and lobing of the margin of the wings seem to have both a genetic as well as a developmental basis for their expression. This is evident because of their variation from plant to plant as well as in the same individual. The presence or absence of wings and of pubescence are also probably under genetic control. The wingless form was named *C. aphanopterus* by Gray from material of the Wilkes Expedition collected at Obrajillo, Peru. It is probably significant that certain specimens collected at the same time have winged fruits and perhaps were part of the same population.

A great amount of variation in these characteristics has been observed among the individuals of the same collection which obviously represent the same population. Examples illustrating variation in the wing development, ranging from presence to absence, are found in the following collections: *Ferreyra 7279* (GH), *Ferreyra 8945* (GH), and *Ferreyra 7520* (US). Examples illustrating variation in pubescence are found in the following collections: *Ferreyra 8945* (GH), *Ferreyra 6088* (US), *Ferreyra 7520* (US), *Macbride* and *Featherstone 467* (F) and *Pennell 14398* (NY).

The great variability within this species is clearly shown by a study of the more recent collections. All present information indicates that the names given in the synonymy list apply to variants of *C. chilensis*. Placing them in synonymy is the only reasonable course of action if the close intergradations of the morphological variants are taken fully into account. More information, particularly of a cytogenetic nature, is highly desirable and perhaps would permit a more precise taxonomic treatment of what appears to be a rather complex assemblage of minor variants.

The origin of the type material of *C. chilensis* collected by Lagasca is given as "chili" by De Candolle. We have not seen the type, but the illustration accompanying the original description reflects a similarity to specimens from Peru rather than any we have seen from Chile. Lagasca, in describing *Biscutella cuneata*, which presumably was based on the same original material, merely gives, "Habitat in America meridionali." It is suspected that the type of *C. chilensis* came from what is now Peru rather than from Chile. The scarcity of *C. chilensis* in Chile is indicated by the fact that other than an early Dombey collection which may actually have been gathered in Peru, we have seen only one other collection, that of Ricardi, Marticorena and Matthei from over 10,000 ft. in the Department of Arica.

DISTRIBUTION: Northern Argentina, Bolivia, northern Chile, Peru.

PERU: Andes of Peru, Wilkes Exped. (GH, type; isotype of *C. pinnatifidus* var. *integrifolius* Gray); without locality, 1837, *Dombey 619* (G). La Libertad: Canduay, Sinsicap (Prov. Otuzco), 2750 m., May 1, 1954, *A. Lopez M. 1059* (US); Chiputur Mountains (Trujillo), 400 m., August 1949, *A. Lopez M. 368* (GH). Ancash: near San Rafael between Casma and Huarmei (Prov. Santa), sandy soil among boulders, 400 m., September 17, 1938, *Stork et al. 9160* (GH, UC); Lomas de Casma (Prov. Santa), rocky mountain slopes, 400-500 m., September 9, 1950. *Ferreyra 8060* (GH, US); Huancar above Chiquian (Prov. Bolognesi), on clay between scattered bushes, 3820 m., April 15, 1949, *Ferreyra 5757* (GH, US); Casca above Chiquian (Prov. Bolognesi), on stony clay, 3100-3200 m., May 9, 1950, *Ferreyra 7279* (GH, US); Jerusalem (Prov. Bolognesi), clay slopes, 3200-3250 m., May 18, 1950, *Ferreyra 7520* (GH, US); Huancar above Chiquian (Prov. Bolognesi), on clay, April 15, 1949, *Cerrate 208* (GH); Mahuay (Prov. Bolognesi), foot hills, May 22, 1954, *Cerrate 2228* (GH). Lima: Ambar (Prov. Cajatambo), annual rainy season herb on gravelly hill side, 2010 m., April 16, 1939, *Stork 11441* (GH, UC); Obrajillo, Wilkes Expedition (GH, type; US, isotype, *C. aphanopteris* Gray); above Obrajillo along Rio Chillón, rocky slopes, 2800-3200 m., June 13-23, 1925, *Pennell 14398* (F, GH, NY, US); San Buenaventura, wet shaded banks beside streams, 2700-2900 m., *Pennell 14588* (F); Huaros, bushy slopes, 3200-3400 m., June 23, 1925, *Pennell 14702* (F, GH, NY, US); Matucana, moist soil among rocks on steep western slope, about 8000 feet, April 12-May 3, 1922, *Macbride and Featherstone 84* (F, US); Matucana, rocky slope, 8,000 ft., April 12-May 3, 1922, *Macbride and Featherstone 112* (F, NY); Matucana, moist swales on northern mountain side, about 8,000 ft. April 12-May 3, 1922, *Macbride and Featherstone 211* (F, type; NY, isotype of *C. Paysonii* O. E. Schulz); Matucana, upland slopes, 8,000 ft., April 12-May 3, 1922, *Macbride and Featherstone 428* (F, GH); Matucana, steep moist eastern slope, 8,000 ft., April 12-May 3, 1922, *Macbride and Featherstone 467* (F); Matucana, rocky, grassy shady slope, 8,000 ft., April 12-May 3, 1922, *Macbride and Featherstone 557* (F, GH); Matucana (Lima-Oroya rail road), 2400 m., 1910, *Weberbauer 5256* (F, GH, US); between Matucana and Tambo de Viso (Prov. Huarochiri) April 9, 1910, *Weberbauer 5209* (F); Viso, shallow soil on rocks about 9,000 ft., May 5-14, 1922, *Macbride and Featherstone 601* (F, NY); Viso, sandy sunny soil, 2800 m., April 23, 1929, *Goodspeed et al. 11518*, (GH, UC); Rio Blanco, decomposing rock outcrops, 12,000 ft., May 8-19, 1922, *Macbride and Featherstone 696* (F, NY) and *697* (F, GH); Rio Blanco, between San Mateo and Casapalca (Prov. Huarochiri), rocky mountain slopes, 3,500-3,550 m., May 25, 1950, *Ferreyra 6975* (GH); Rio Blanco, between San Mateo and Casapalca (Prov. Huarochiri), evergreen mountain forests, 3300-3400 m., March 9, 1953, *Ferreyra 8945* (GH); Rio Blanco, open hill side, 3,000-3,500 m., April 15-17, 1929, *Killip and Smith 21685* (US) and *21700* (NY, US); Cerros de Surco, clay mountain slopes, 2100-2200 m., April 4, 1946, *Ferreyra 640* (US), Picoy, above Surco, slopes of mountains 3200-3300 m., May 22, 1949, *Ferreyra 6088* (GH, US); near Surco, 2100-2200 m., April 3, 1955, *Ferreyra 10529* (GH); near Chicla, 12,000-13,000 ft., April 1-23, 1882, *Ball* (GH, NY). Arequipa: Volcan de Misti, moist rocky walls of canyon, 3300-3400 m., April 11, 1925, *Pennell 13223* (F, GH, NY, US). Maquega: Carumas, 3200 m., February 21-March 6, 1925, *Weberbauer 7281* (F, US); Torata, 2700 m., March 17-18, 1925, *Weberbauer 7416* (F, US). BOLIVIA: Prov. Larecaja near Torata, rocky cliffs, sub alpine, 3700 m., March-April 1960, *Mandon 905* (F. GH, NY, isotypes of *C. parviflorus* Wedd.) ARGENTINA: Tucuman. Estancia Las Pavas-Cerro Boyo (Dept. Chicligasta), over rocks, May 12, 1924, *Venturi 3102* (US); Penas Azules-Sierras Calchaquies (Dept. Tafi), 3400 m., January 29, 1933, *Burhart 5281* (SI). CHILE: Dombey (photo at F); Subida al Portezuela de Chapiquiña, Dept. Arica, Prov. Tarapaca, 3360 m., March 26, 1961, *Ricardi, Marticorena and Matthei 157* (CONC, GH).

6. **Cremolobus stenophyllus** Muschler Engl. Bot. Jahrb. 50. Beibl. **111**:7. 1913

Loxoptera stenophylla (Muschler) Schulz, Bot. Jahrb. **66**:93. 1933

Annual herbs, 25-30 cm. high; stems branched profusely, angulate, glabrous throughout; leaves alternate, linear, 4-5 cm. long, less than 0.7 cm. broad, dentate, acute, glabrous on both sides, short petiolate, petioles very slender; pedicels about 1 cm. long when fully mature, horizontal, sigmoid, minutely pubescent; sepals greenish, oblong, ca. 2 mm. long, hyaline margined, inner pair deeply keeled with a broad base; petals white, clawed, 3-3.5 mm. long, entire; nectaries 4, poorly developed; stamens distinctly tetradynamous, filaments uniform in breadth throughout, up to 3 mm. long in paired stamens, anthers sagittate; gynoecium supported on a thin gynophore which may be of the same length as the style in mature fruit; style rigid, conical elongated, stigma slightly broader in diameter than that of the style, separated from the style by a distinct constriction; valves slightly directed downwards with respect to replum, orbicular, 2.5-3.0 mm. across, glabrous, wings very well developed, thin, translucent, sometimes rolled over at the edges, margin entire to slightly wavy, minor cross wings present in the center on both sides of the valves, extent of development variable, minor wings curled inward forming a pouch like structure; seeds elongate orbicular, attached by a thin funicle, ridged in the position of the cross wings, dark brown; cotyledons accumbent. Fig. 3.

PERU: Mountains near Chosica (Lima-Oroya railroad), 1400-1500 m., April, 1910. *Weberbauer 5335* (Isotypes: F, GH, US); near Lima, July 5, 1914, *Rose 19479* (US).

Schulz (1933, 1936) treated *Cremolobus stenophyllus* as a separate genus, *Loxoptera,* on the basis of a number of presumed distinctive characters such as the orientation of the nectaries, the heart-shaped anthers, the gynoecium being longer than the paired stamens, the long and thin style, the stigma being smaller than in other species of *Cremolobus* and the development of the minor wings on the valves. The heart-shaped anthers are not characteristic of this species alone. The relative length of the stamens and gynoecium is a variable feature, the latter being influenced considerably by the age of the flower. The long and thin style and the size of the stigma is similar to that of other species of *Cremolobus.* The only major character which distinguishes this species from others of *Cremolobus* is the presence of secondary wings on the valves. The extent of secondary wing development is variable as may be seen by observing different specimens of the same population. Unfortunately, the available material of the species is too meagre to permit an assessment of the full range of variability of this character. However, it is pertinent to mention here the parallel situation in the related genus *Menonvillea.* In a previous study of *Menonvillea* (Rollins, 1955), specimens with 6 and 10 winged fruits (formerly known in the two genera, *Hexaptera* and *Decaptera,* respectively) were shown to be present in the same collection. The partial development of secondary wings in *Menonvillea scapigera* was also stressed. On this basis it was concluded, "that the presence or absence of additional wings may not be of marked significance." Because the extent of wing development did not coincide with other significant natural generic boundaries, *Hexaptera* and *Decaptera* were merged into the single genus *Menonvillea*. A similar treatment is indicated by the evidence for the present case as well. Thus, the generic name *Loxoptera* is not maintained.

In the four sheets of specimens we have for study, the leaves are shallowly dentate to entire and the lower ones in particular have a very slender petiole. The branching is all well above the base and it appears that no truly basal leaves are produced. Plants of this species are undoubtedly rapid growers, presumably responding to moisture for their growth period more than to season.

7. **Cremolobus rhomboideus** Hook., Icon. Pl. t 32. 1837

Urbanodoxa rhomboidea (Hook.) Muschler, Bot. Jahrb. **40**:271. 1908.

Annual herbs, up to 1.25 m. tall; stems rather sparingly branched in the upper region, glabrous throughout; leaves alternate, tending to be opposite on the lowermost portion of the stem, short petiolate, rhomboidal to ovate-lanceolate, 2.5-3.0 cm. long, 1-1.5 cm. broad, serrate acute, glabrous; pedicels very short when young, up to 2 cm. when mature, divaricate, minutely pubescent on the upper side; sepals ca. 1.5 mm. long, outer pair less hollow than inner and attached by a narrow base; petals spatulate, not sharply clawed, 2.5-3.0 mm. long; stamens long and short, longer ones 2 mm. in length, anthers heart-shaped, sagittate; gynoecium supported on a thin gynophore; style thick, conical elongated when mature, stigma about the same as the style in diameter; valves narrowed to a limited point of attachment on the lower side of the replum swelling, valves ca. 4 mm. long, 3 mm. across, wingless, rugose, dentate, pubescent; seeds attached by a distinct funicle, flat, 2 mm. across; cotyledons accumbent. Fig. 1.

PERU: Carumas (Prov. Moquegua), 3,200 m., February 21-March 6, 1925, *Weberbauer 7296* (US); Viso, about 9,000 ft., May 5-14, 1922, *Macbride and Featherstone 572* (NY).

Muschler (1908) separated *C. rhomboideus* from *Cremolobus* and erected the monotypic genus *Urbanodoxa*. The stated basis for this course of action was the absence of alternate leaves, the presence of poorly developed nectaries, and the lack of development of the wings on the valves. These features, he thought, were distinctive as compared to the usual characteristics of *Cremolobus*. Essentially the same treatment was further elaborated by Schulz (1936), who ascribed a number of additional characters to *Urbano-*

doxa that were purported to be different from *Cremolobus.* These included the presence of a gynophore nearly of the same length as the elongated conical style, the triangular valves not keeled or winged and the presence of radial nerves or wrinkles on the valve surfaces.

An examination of all these characters in relation to the other species of *Cremolobus* shows that they all occur to a varying degree throughout the genus. None of them, either singly or in combination, provides the distinctiveness required to support this taxon at the rank of a genus by itself. The leaves of *C. rhomboideus* are not always opposite as suggested by Muschler, they are opposite only on the lower portions of the stem or in the younger plants. Other species of *Cremolobus* are not characterized entirely by alternate leaves. Two very distinct species, *C. bolivianus* and *C. subscandens,* invariably have opposite leaves. The nectaries, though very small and inconspicuous in most species of *Cremolobus*, may be quite large in others, particularly those having large flower size, as in *C. peruvianus* and *C. suffruticosus.* Most of the species of *Cremolobus* have the gynoecium raised on a thin gynophore which is nearly as long as the style. Furthermore, the style is conical in *C. suffruticosus, C. chilensis* and *C. stenophyllus.* In some variants of *C. chilensis,* the distinction between the diameter of the mature style and that of the stigma is only slight. The triangular shape of the valves with radial veins and ridges and the complete lack of the wings is comparable to certain forms of *C. chilensis with* suborbicular triangular valves with almost no wings. The size of the fruit in *C. rhomboideus* is larger than in the wingless forms of *C. chilensis,* and the texture is much harder, but these characters alone hardly justify generic rank for *C. rhomboideus.*

The weak segregation of *Urbanodoxa* from *Cremolobus* was pointed out by Macbride (1938). Actually, the distinctive features of *C. rhomboideus* make it a clearly marked species, but the combination of features it possesses place it unmistakably with the other species here included in *Cremolobus.*

SPECIES EXCLUDED

A special comment on the name *Cremolobus linearifolius* H. & A. (Hook. Bot. Misc. 3: 138. 1833) is required. This name is based on Cuming 905 collected at Coquimbo, Chile;

and a fragmentary specimen which apparently is the type is now in the herbarium of the University of Glasgow. A photograph of the type has been examined. The plants are somewhat comparable in habit to the smaller forms of *C. chilensis* with linear, ribbon shaped and deeply pinnatifid leaves. However, no complete fruits are present on the specimens. The valves are missing but the gynophore, the replum with two lateral points of valve attachment and the conical style could refer to either *Menonvillea* or *Cremolobus*. We cannot be absolutely sure of the generic identity of this taxon at the present time. However, we feel confident, from the evidence discernable on the photograph of the type, that it is *Menonvillea* and not *Cremolobus*.

The association of *C. linearifolius* with *C. rhomboideus* [*Urbanodoxa rhomboidea* (Hook.) Muschler] as suggested by Schulz (1936) is certainly not the proper disposition of the name. In *Menonvillea*, *Cremolobus linearifolius* could apply to the species we have referred to by the name *M. Gayi* Ph., or it might possibly be the same as *M. chilensis* (Turcz.) Jackson. The type is so fragmentary that a very careful examination will need to be made, and even then it may not be possible to fix the application of the name *C. linearifolius* with certainty.

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THE TAXONOMY OF THE SALIX GLAUCA COMPLEX IN NORTH AMERICA

THE TAXONOMY OF THE SALIX GLAUCA COMPLEX IN NORTH AMERICA[1]

GEORGE W. ARGUS[2]

The species in the *Salix glauca* L. complex have long been recognized as a source of taxonomic difficulties in northern botany, and more than one student has commented on the variation within the group and urged a detailed study. In the Flora of Alaska and Yukon, Hultén (1943) observed that "The many closely related forms of the *S. glauca* group in arctic and subarctic America, *S. brachycarpa, S. glauca, S. glauca desertorum, S. cordifolia, S. anamesa, S. pseudolapponum* and others are very much in need of thorough study." The confusing variation occurring in these species was commented on by Polunin (1940) who noted that in arctic Canada intermediates occur linking *S. glauca* and *S. cordifolia* var. *callicarpaea* and ". . . a continuous series could probably be constructed connecting almost all the Salices of our region, . . ." In 1959, Raup wrote "I do not think that the taxonomic realities in *S. glauca* or in the group of entities related to it will be understood until the full range of their variability is better known, and until we have some light on its causes."

One of the purposes of this study was to contribute to a knowledge of the variation in the *Salix glauca* complex, suggest some possible causes for the unusual variation present, and to introduce a measure of order into the classification of the American taxa, thereby starting a much needed study of this important group of circumpolar willows.

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The question of whether "true" *Salix glauca* L. occurs in the Western Hemisphere has been considered by Raup (1931, 1943, and 1959), Polunin (1940), and Hultén (1943) and will not be considered in detail in this paper. These authors concluded that at least some of their American material was identical to *S. glauca* of Europe. The variation in the European material of *S. glauca* that I have studied is very similar to that in American material, and I am of the opinion that *S. glauca* is widespread in America. However, until comparative population samples are available, and further cytological study is done a discussion of this question is mainly speculative.

The present study of *Salix glauca*, a circumpolar species ranging in the Western Hemisphere from Alaska to Newfoundland and Greenland, and south in the Rocky Mountains to New Mexico, was restricted to North America for several reasons. First, this area was in particular need of study; second, it was relatively accessible; and third, the amount of herbarium material available from this area alone was overwhelming. I have been aware of the pitfalls of a restricted study of a widespread taxon and the inadequacy of my familiarity with the Eurasian *S. glauca* and its relatives. For this reason, as much as any other, my taxonomic treatment of the circumpolar *S. glauca* differs from that of the American *S. brachycarpa*. In *S. glauca* the variation has been described in detail and related to geography, but no formal taxonomic categories have been proposed, whereas, in *S. brachycarpa* infraspecific status has been assigned to several geographic variants.

Throughout the study every effort was made to consider the taxa in terms of populations exhibiting genetical, ontogenetical, ecotypic, and ecophenic variation. The sampling of local populations in the field and the herbarium has contributed to an understanding of population variation, and the degree of ontogenetic variation to be expected in individuals was studied in successive collections of tagged plants. The cultivation of cuttings has contributed to an understanding of phenotypical plasticity, and several artificial hybridizations have pointed to the value of further such studies. More information for almost every aspect of the problem is needed and further studies in cytology, hybridization, and morphology are certain to modify and supplement the conclusions presented here.

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THE SALIX GLAUCA COMPLEX: ITS CHARACTERISTICS, COMPOSITION, AND INTRAGENERIC POSITION

Characteristics. The species belonging to the *Salix glauca* complex can be recognized by the following combination of characteristics: low shrubs, 3-6 feet tall, or sometimes prostrate, with pubescent branchlets. Leaves glaucous and pubescent beneath and pubescent to glabrate above; margin entire. Flowers arranged in coëtaneous aments borne on short leafy reproductive shoots (peduncle of authors). Bracts of the flowers light brown to yellowish, pubescent. Staminate flowers with two stamens, filaments pubescent, subtended by an adaxial and an abaxial gland. Pistillate flowers with a pubescent ovary subtended by an adaxial gland.

Composition. Fundamentally, the *Salix glauca* complex in the Western Hemisphere consists of two highly variable species, *S. glauca* and *S. brachycarpa.* A multitude of names has been applied to these two taxa and their various forms, including *S. desertorum, S. glaucops, S. pseudolapponum, S. cordifolia, S. callicarpaea, S. villosa, S. anamesa, S. niphoclada, S. muriei,* and *S. fullertonensis,* and numerous infraspecific names. These names and others are discussed in the sections on synonymy. Other species including *S. wolfii,* its var. *idahoensis,* and *S. eastwoodiae* (incl. *orestera*) seem to be closely related to this complex and further study may include them.

Intrageneric Position. To place the *Salix glauca* complex in its proper intrageneric position is difficult and hazardous because of the fragmentary nature of our knowledge of the affinities within the genus. The subdivision of *Salix* into sections is generally unsatisfactory, and many of the commonly recognized sections are clearly artificial. However the following review of the historical development of the intrageneric classification of *Salix* will provide a background for further study. Throughout this review emphasis is placed on the *Salix glauca* complex, although related taxa will be discussed.

Attempts to subdivide the genus *Salix* into intrageneric units have great antiquity. Even prior to Linnaeus, who in 1737 and 1753 presented a classification based on stamen number and leaf characteristics, Theophrastus and Plinius proposed subgeneric groupings.

Muhlenberg (1805) was the first author to treat the North American willows. In this treatment, which did not include species related to *Salix glauca,* he subdivided the genus into two groups, those with leafy peduncles, and those with naked peduncles.

Between 1825 and 1828 "natural" classifications were proposed by Dumortier, Fries, and Koch. Dumortier (1825) described five sections and grouped them into two series based on, 1) stamens coming from the side of the nectary, and 2) stamens coming from the center of the nectary.

Fries presented his first classification of *Salix* in 1825. It was followed in 1828 by a second treatment, assumed to be the same as his 1825 treatment (Toepffer, 1915), in which he based his primary classification on whether the capsules were sessile or pedicellate, with a further subdivision relating to the height of the plants. In this treatment tribe *Glaucae* included *S. lanata* L., *S. glauca*, *S. limosa* Wahl., and *S. versifolia* Wahl.

The same year, but after Fries, Koch (1828) classified the European willows using as primary subdivisions, 1) sessile aments produced at the tip of a branchlet, with leaves from buds below the aments; 2) "pedunculate" aments produced from the tip of the previous years branchlets, peduncle increases in size and bears leaves with buds in the axils; and 3) terminal bud, and generally others beneath it, producing vegetative shoots, the aments originating beneath these. Further subdivision was based on bract-color, anther-color, and pedicel-length. His cohors *Frigidae* included *S. limosa*, *S. glauca*, *S. pyrenaica* Gouan, *S. waldsteiniana* Willd., *S. prunifolia* Sm., *S. caesia* Vill., *S. myrsinites* L., and *S. jacquinii* Hort.

Hooker (1830) in his British Flora used a classification suggested by Borrer. In it *Salix* was divided into equal units previously used by Dumortier, Fries, or Koch; however, some were originated by Borrer. Three species, *S. glauca*, *S. arenaria* L. and *S. stuartiana* Sm., were included in *Glaucae*. No rank was assigned to these groups; however, later authors assumed they were sections (Toepffer, 1915), and in some treatments Borrer's name appears as the author of these "sections".

Fries in 1832 and again in 1840 revised his original classification, drawing on the work of Dumortier and Koch. In 1832 he erected tribe *Amerina* (sect. *Amerina* Dumortier) and included in it species with pedunculate aments borne on lateral twigs. This included: *S. pentandra* L., *S. amygda-*

lina L., *S. fragilis* L., *S. viridis* Fries, *S. alba* L., *S. glauca*, and its varieties *appendiculata* Wahl., *nivalis* Wahl., and *pallida* Fries. The artificiality of this tribe was recognized and in 1840 he again modified his classification. *Salix glauca* was placed in *Chamelix-Frigidae* (rank undesignated) with *S. glauca* var. *pullata* Laest., *S. glauca* var. *pallida*, *S. arbuscula* L., *S. myrsinites* L., and *S. pyrenaica* var. *norvegica* Fries.

Trautvetter in 1833 expanded Koch's cohors *Frigidae* by combining it with cohors *Chrysantheae*. The following names were included in this emended taxon: *S. arenaria*, *S. lanata*, *S. glauca* and vars. *microcarpa* Ledeb., and *macrocarpa* Ledeb., *S. arctica* Pall., *S. myrsinites*, *S. prunifolia* Sm., *S. sibirica* Pall., and *S. brayi* Ledeb.

The willows of North America were arranged in groups by Barratt in 1834, but this treatment was unpublished until 1838 when part of it was used by Hooker in Flora Boreali-Americana. Finally, in 1840 a revised and shortened edition of this classification was published by Barratt. His classification closely followed that of Borrer, but several new groups were erected to contain American species.

In 1836 Trautvetter radically revised his infrageneric classification of *Salix*. He divided the genus into two taxa *Chrysolepideae* and *Allolepideae* based on bract-color. Within the former he recognized two subdivisions based on bract-persistence and within the latter he recognized four subdivisions based on leaf-texture and shape. The group *Platyphyllae* included *S. glauca*, *S. glauca* var. *melanolepis* (Ledeb.) Trautv. *S. phylicifolia* L., *S. hastata* L., *S. arbuscula*, *S. arenaria*, *S. aurita* L., and *S. caprea* L.

Before Barratt's manuscript on the North American willows was published it was used extensively by Hooker (1838). Names which are now regarded as part of *Salix glauca*, *S. desertorum* Richards. and *S. cordifolia* Pursh, were placed in different sections. *Salix desertorum* was placed in sect. *Arbusculae*, small shrubs of the arctic and alpine, with coëtaneous aments; and *S. cordifolia* in sect. *Prostratae*, low shrubs of arctic and alpine areas, aments coëtaneous and pedunculate. Both groups contained unrelated species.

In his Flora Rossica, Ledebour (1850) gave the cohors of Trautvetter the rank of section for the first time. In sect. *Frigidae*, he included *S. lanata*, *S. lapponum* L., *S. glauca*, *S. reptans* Rupr., *S. arctica*, *S. myrsinites*, *S. ovalifolia* Trautv., *S. arbuscula*, *et al.*

In 1858 N. J. Andersson treated the North American willows following the 1840 classification of Fries. In *Chamaelix-Frigidae* he included *S. glauca*, its var. *villosa* Hook., *S. desertorum*, *S. arctica* R. Br., *S. subcordata* Anderss., *S. alpestris* Anderss., *S. myrsinites*, *S. pseudomyrsinites* Anderss., *S. curtifolia* Anderss., *S. arbuscula*, *S. rhamnifolia* Hook., *S. ovalifolia*, and *S. glacialis* Anderss. In 1867 Andersson began a revision of the classification of the willows of the world which was completed in De Candolle's Prodromus in 1868. In this treatment the classification was based primarily on stamen-number and secondarily on style-length, and geographic distribution. *Salix glauca* and its relatives were placed in *Niveae* s. *Glaucae* c. *Sericeae* Anderss. Included in this group were *S. glauca* and its vars. *sericea* Anderss., *pullata*, *virescens* Anderss., *alpina* Anderss., *S.* × *glaucops* Anderss., and its var. *villosa* (Hook.) Anderss., and var. *glabrescens* Anderss., *S. desertorum* and its vars. *elata* Anderss., var. *stricta* Anderss., and *fruticulosa* Anderss., *S. lingulata* Anderss., *S. pyrenaica*, *S. reptans*, *S. subcordata*, and various hybrids.

Wichura in 1865, after a lengthy dissertation on hybridization in the genus *Salix*, proposed a classification which ". . . brought the true species into natural groups." His general classification did not find much support but his use of the nectary-number as a diagnostic characteristic did.

Nectary number was used by Otto von Seemen (1903) in his treatment of *Salix* in Salices Japonicae. His first division was based on the number of nectaries in the staminate and pistillate flowers; further subdivision was based on the number of stamens, whether they were united or not, and on style-length. His infrageneric classification was used by C. Schneider (1904) in his Handbuch der Laubholzkunde, and by A. Toepffer (1915) in Salices Bavariae. The use of nectary-number by Schneider resulted in the unnatural separation of *S. desertorum* from *S. glauca*. *Salix* *glauca*, *S. pyrenaica*, and *S. arctica* were placed in sect. *Sericeae* Koehne (Deutsche Dendrol., 1893) and *S. desertorum* was placed in sect. *Lanatae* Koehne subsect. *Villosae* Anderss. along with *S. lapponum* and *S. helvetica* Vill.

In the late 19th and early 20th century the taxonomy of North American *Salix* received an unprecedented amount of attention. Prominent among the students of the genus were M. S. Bebb, P. A. Rydberg, C. R. Ball, and C. Schneider. In Coulter's Manual of the Botany of the Rocky Mountain Region, M. Bebb (1885) presented a synoptic key to *Salix*. Under the headings, "Aments lateral or terminal with or without bracts: scales persistent, usually darker at the tip: stamens 2; filaments glabrous - capsules tomentose - pedicels short or none - styles distinct" he included the following names: *S. chlorophylla* Anderss., *S. candida* Willd., *S. glauca* var. *villosa*, *S. desertorum*, and its var. *wolfii* Bebb, *S. arctica* R. Br., and its var. *petraea* Anderss.

Rydberg (1899) was disturbed by Bebb's conservative approach to the species of western America and felt that, "*S. desertorum* and *S. reticulata*, as understood by him (i.e. Bebb), consist . . . of at least three species each." Rydberg was of the opinion that characteristics of significance to *Salix* were not being properly regarded. He stated ". . . if characters generally accepted as good by European salicologists should be applied to American species, . . . the number of our native species would be doubled." In applying this reasoning to the arctic and Rocky Mountain species Rydberg multiplied the American species of *Salix* at a rapid rate. Most of his taxa have since been reduced to synonymy or to infraspecific rank. In his 1899 treatment he described a new group, *Arcticae*, to include "Caespitose willows, . . . with entire-margined leaves, catkins at the ends of short leafy branches, appearing with the leaves, more or less densely white-tomentose or villous capsules and an evident style." This group was very large primarily due to the many new species described by Rydberg. Undoubtedly several of the taxa included in the *Arcticae* do not belong there, but he was probably correct in including the *S. glauca* complex and the *S. arctica* complex in the same group.

In his Flora of Colorado Rydberg (1906) added *Salix chlorophylla*, and *S. pseudolapponum* v. Seem. to the *Arc-*

ticae, and changed the name of *S. stricta* to *S. brachycarpa* Nutt.

Three years later C. Ball (1909), treating *Salix* for Coulter and Nelson's Flora of the Central Rocky Mountains, used Rydberg's sub-generic units, adding *S. candida* to the *Arcticae* and transferring *S. chlorophylla* to the *Phylicifoliae*.

Rydberg (1917) expanded his concept of the *Arcticae* in the Flora of the Rocky Mountains and the Adjacent Plains to include *S. idahoensis* (Ball) Rydb., *S. subcordata*, *S. austinae* Rydb., *S. maccalliana* Rowlee, *S. saskatchewana*, *S. cascadensis* Cock. and *S. nelsonii* Ball.

During 1912 and 1914 treatments of *Salix* were published which provided rank for many intrageneric units that had been used in the past without designated rank. The first was Frye and Rigg (1912) who assigned the rank of subgenus to Rydberg's sub-generic units, and the second was C. Moss (1914) who, in the Cambridge British Flora, named four sections, *Amerina*, *Chamaetia*, *Vetrix*, and *Vimen*, and described series within each of them. Series *Glaucae* was used to include the species of the British flora related to *S. glauca*. This treatment was followed by Rehder in 1949.

C. Schneider, a German citizen interned in the United States during World War I, was permitted to continue his botanical studies at the Arnold Arboretum under the supervision of C. Sargent. From 1918 to 1921 he published his outstanding monograph of the American willows, a treatment which was to provide the basis for much of the later work on American *Salix*. In 1921 he summarized his classification, which had appeared previously in twelve separate papers, and noted that stamen-number provided a basis for recognizing two large natural groups within *Salix*. One of these groups he named *Pleiandrae* and the other was left unnamed. No rank was assigned to these groups. The section was his primary sub-generic taxon. Schneider's work has played a prominent role in the formulation of our present day concepts of the genus. However, it should be noted that his idea of a section was a narrow one and often corresponds to the species complex. He wrote ". . . I thought it best not to unite species of apparently no close affinity in the same group but to propose new sections for those species which show good characters." In his treatment of *S. glauca* and related species (Schneider, 1918b) he used sect. *Glaucae* to include the species of the *S. glauca* complex and sect. *Ovalifoliae* to include the *S. arctica* complex. In the discussion of differences between *Glaucae* and *Ovalifoliae* he noted the difficulties involved but felt that the bracts were of diagnostic significance. He characterized sect. *Glauca* as having bracts uniformly yellowish, light-brown or straw-colored compared with the bicolored bracts of sect. *Ovalifoliae* which tend to be pale at the base and dark-brown, fuscous, or even black at the apex. Furthermore, the pubescence of the bracts in *Glaucae* was shorter, less straight and rarely distinctly silky in contrast to the long straight, silky hairs on the bracts of the *Ovalifoliae*.

Floderus (1931) in Holmberg's Skandinaviens Flora proposed a classification utilizing sections and series of Dumortier to divide the genus into three groups, *Chamaetia*, *Caprisalix*, and *Amerina*. Under *Caprisalix* he listed *Glaucae* Fries which included *S. glauca*, *S. stipulifera* Flod. and a host of hybrids. This classification was followed closely by Nasarov (1936) in the Flora USSR. Nasarov assigned subgeneric status to the three main groups used by Floderus and sectional rank to their subdivisions. In section *Glaucae* he included the following species: *S. glauca*, *S. stipulifera*, *S. seemannii* Rydb., *S. altavica* Kar. & Kir., and *S. reptans*. He also used sect. *Arcticae* of subgenus *Chamaetia* to include *S. arctica*, *S. torulosa* Trautv., *S. pallasii* Anderss., *S. pulchra* Cham. and *S. divaricata* Pall. Hultén (1943) followed essentially the same sectional classification as Komarov and placed the species related to *S. glauca* in sect. *Glaucae* and those related to *S. arctica* in sect. *Arcticae*. He correctly transferred *S. pulchra* from sect. *Arcticae*, where it was assigned by Nasarov, to sect. *Phylicifoliae*.

In his studies of *Salix*, Raup (1943, 1959) has regarded the formal sectional category with some skepticism. In 1943 he wrote "Neither in the arrangement of the list nor in the keys have I indicated sectional subdivisions of the genus. With our present understanding of the relationships, past and present, among the species, it is somewhat hazardous to do so." However, he did give a list of the tentative sectional disposition of his species. In 1959 he made a further break with the use of formal infrageneric taxa by placing the taxa into groups named after the major species of the group. Many of these were species complexes. However, despite the reluctance to use sectional categories Raup did list informal categories in the general order of the sections as they were used by C. Schneider.

This skepticism seems justified in view of the diversity of opinion concerning the alignment of species within *Salix* and the lack of reliable diagnostic characters on the subgeneric level. The characters used as diagnostic for subgeneric taxa have included habit (Hooker), branching pattern (Koch), nectary-number (Wichura), bract-color and -persistence (Trautvetter), stamen-number (Andersson) *et al.* These criteria generally have been inadequate for the purpose either because of their variability or because of inadequate study. A complete subgeneric revision of *Salix* based on thoroughly studied meaningful characters is much needed.

The infrageneric rank of the species related to *Salix glauca* may be treated in two general ways. They may be placed in a narrowly conceived sectional group which should be named *Salix* sect. *Glaucae* (Fries) Schneider, or in a broadly conceived section named *Salix* sect. *Frigidae* (Koch emend. Trautv.) Ledebour. The treatment depends on whether or not the author believes *Salix glauca* and *S. arctica* should be placed in the same section. There is precedent for each view, with Trautvetter, Ledebour, Bebb, and Rydberg placing these species in the same group and Andersson, Schneider, Floderus, and Hultén placing them in different groups. In my opinion the broadly conceived section, *Salix* sect. *Frigidae*, is the more natural taxon. However, my earlier statement on the difficulty of making infrageneric assignments and our lack of information remains pertinent.

TECHNIQUES

Population Sampling. Two types of population-samples were used to analyze variation, 1) the field local population, and 2) the "herbarium local population." In both types of populations the unit sampled was defined in terms of a taxon, a geographic area, and the seasonal development of reproductive structures. In the field local population samples habitat was an additional criterion.

The field local population of a taxon was sampled in a small geographic area of relatively homogeneous vegetation and habitat. A single shoot bearing reproductive structures was selected from each of about 100 plants. Randomness was achieved by the use of a grid in which a sample was taken every 25 paces (used at Churchill, Manitoba and Lake Athabasca, Sask.) or by "unselectively" collecting a sample as the taxon is encountered in walking through an area. The latter method is less objective than the former, but it is applicable to areas in which the taxon is sparsely distributed or where time is limited. Such local population samples are of the "mass collection" type described by Anderson (1941).

The "herbarium local population" was sampled by assembling herbarium specimens of a taxon from a particular geographic area and selecting out all specimens in a comparable stage of ontogenetic development. In this study each specimen was in anthesis or early postanthesis and bore mature leaves. No attempt was made to segregate specimens on the basis of habitat and the range of habitats represented in each set of samples approximated the range of local habitats occupied by the taxon. The size of the geographic area and the number of specimens studied varied with the intensity of local collecting. However, the geographic area was kept as small as possible and the sample size as large as possible.

The value of the "herbarium local population" in determining the mean and range of variation in a taxon can be illustrated by comparing the variation based on a herbarium-sample of 27 specimens from Churchill, Manitoba (population 15., figs. 21, 23, and 25) with field local population samples of 100 specimens from the same area (figs. 1 and 9). The degree of variation and the estimated mean values are similar in each case and for the purposes of this study are not significantly different.

Morphological Measurements. In order to obtain comparable measurements an effort was made to measure organs from the same position on the plant and in the same stage of development. Measurements of leaf-blade, petiole, and stipule dimensions were based on the largest mature leaf on the shoot. Measurements were made using a millimeter scale without magnification, except in the case of stipule measurements and the short petiole in *Salix brachy-*

carpa in which 9× magnification was used. Ament and flower dimensions were measured using a millimeter scale and 9× magnification. Ament length was measured from the base of the lowermost flower to the apex, and width was measured near the middle of the ament. Ovary, capsule, pedicel, and bract-length were measured on several flowers selected from near the middle of the ament.

Stomatal Measurements. In the stomatal studies leaves were examined from dry herbarium specimens. In each case one or two mature leaves were selected from the distal end of the shoot. In two specimens all the leaves from several annual shoots were removed and studied.

The leaves were cleared and stained using a modification of the tannic acid — ferric chloride stain (Foster, 1934) as described by Wilson (1958). The clearing was accomplished by treating the leaves in 5% aqueous sodium hydroxide until discolored and then bleaching in 50% aqueous "Clorox." The leaves were washed thoroughly and then treated in 5% tannic acid in 30% ethyl alcohol for about 5 minutes, rinsed and then treated in 5% iron chloride in 30% ethyl alcohol for about 5 minutes. The leaves were then dehydrated and mounted in diaphane. Trichomes were removed by gentle scraping during the 95% dehydration stage.

The length of stomata was determined by measuring 10 to 20 abaxial stomata located near the center of one half of the blade. Measurements were made using a 40× Wild Fluotar objective and a 15× ocular with an ocular micrometer. Drawings of representative epidermal sections were made using a camera lucida and a 44× objective and a 15× ocular.

The Dice-Leraas method of graphically comparing the mean, standard deviation, standard error, and the range of several samples is used in fig. 2. For a modification and a discussion of this method refer to Hubbs and Perlmutter (1942) and Critchfield (1957). The symbols used are: the range, a thin horizontal line; the mean, a vertical line; one standard deviation on either side of the mean, a wide stippled bar; and 2 standard errors on either side of the mean, a solid black bar.

An indication of the "significance" of the differences between any two means can be obtained by comparing the overlap or separation of the two standard errors on either side of the mean. The difference between the means may be considered to be "significant" if the standard error bars do not overlap. The variable sample-size undoubtedly influences the accuracy of this method, and the interpretation of "significance" must be considered with some reservations.

Cytology. Chromosome counts were based on root-tip squash preparations which were fixed and stained essentially as described by Löve and Sarkar (1956). Root-tips were excised and pretreated in saturated aqueous paradichlorobenzene for 3 hours. They were washed and then fixed in 6:3:1 (6 parts absolute alcohol: 3 parts chloroform: 1 part propionic acid) for 12-24 hours and then transferred to 20% ethyl alcohol. The squash and staining process involved the treatment of the material in 45% acetic acid for 1 hour followed by 5-10 min. in equal parts of concentrated HCl and 95% ethyl alcohol. One to two millimeters of the root-tip was excised onto a microslide and stained with ferric acetocarmine. Following gentle heating, the material was firmly squashed under a cover glass. Slides containing good mitotic figures were made permanent and finally studied under a microscope with a 90× oil-immersion objective and 15× oculars. Photomicrographs aided in making the counts and the preparation of drawings. The sectioning of feulgen stained root-tips was tried, but good preparations were not obtained.

Systematic Materials and Methods. The systematic treatment is based on field and herbarium study. Field work was carried out in central Alaska and the Alaska Range; Churchill, Manitoba; Mt. Albert, Quebec; and northern Saskatchewan. Valuable recent collections from the Bering Sea coast of Alaska (Johnson, Viereck, and Melchior) and the Great Slave Lake region (Thieret and Reich) were placed at my disposal by the collectors, and undistributed collections from the Mackenzie Mountains and the Alaska Highway were made available by Prof. H. M. Raup. Special collections of living material from Wyoming (C. L. Porter), Colorado (Levi), Manitoba, and Quebec (Argus) were made for this study.

Herbarium specimens were studied from the following herbaria (the abbreviations are according to Lanjouw and Stafleu (1959) except for GWA, MTSM, and RMNP): Arnold Arboretum (A); University of Alaska (ALA); National Museum of Canada (CAN); Science Service, Dept. of

Agriculture, Ottawa (DAO); Dudley Herbarium, Stanford (DS); Chicago Natural History Museum (F), Thieret and Reich collections only; Gray Herbarium (GH); University of Minnesota (MIN); Missouri Botanical Garden (MO), type only; Michigan State University (MSC), Petrides collections only; Musée de l'Institution des Sourds-Muets, Montreal (MTSM), one specimen; United States National Arboretum (NA); New York Botanical Garden (NY); Rocky Mountain Herbarium, Laramie (RM); Rocky Mountain National Park Herbarium, Banff, Alberta (RMNP); University of Saskatchewan (SASK); University of British Columbia (UBC); United States National Herbarium (US); University of Wisconsin (WIS) and the author's personal collection (GWA). Approximately 7000 specimens were studied.

Range-maps were plotted on Map 202 of Goode's Series of Base Maps, published by the University of Chicago Press. The maps of the phases of *Salix glauca* and the infraspecific taxa of *S. brachycarpa* are for general graphic purposes only, and the limits of the units are only approximate.

The specimens cited here have been selected for a variety of reasons. They may be historical specimens, unusual specimens worthy of note, specimens at the edge of the range of the taxon, specimens referred to in the text, or measured in the geographic variation study of *S. glauca* or in the analysis of the hybrid swarm on Mt. Albert. The symbol "*" after the collector's number indicates that the specimen was measured in either the geographic variation or hybrid study mentioned above. The specimens from Alaska and Yukon are arranged in the districts proposed by Hultén (1941). In other areas political subdivisions have been used.

VEGETATIVE MORPHOLOGY AND BIOLOGY

Stems. The stems of the *Salix glauca* complex are highly branched to form shrubs of variable stature. The tallest shrubs occur in *S. glauca*, which may attain a height of 10 feet. However, the same species may be prostrate under certain environmental conditions, illustrating the great plasticity of this characteristic. At Churchill, Manitoba, prostrate individuals of *S. glauca* were observed on a ridge-top exposed to strong northwest winds and a few yards away, in the lee of a boulder, an erect individual was growing as high as the boulder that was protecting it (figs. 44 & 45). Although such modification is common, one taxon in this complex, *S. brachycarpa* ssp. *niphoclada* var. *fullertonensis*, seems to be habitually prostrate, and *S. brachycarpa* ssp. *niphoclada* is often decumbent. In general, the species of the *S. glauca* complex are erect shrubs about 2 to 4 feet tall.

Shoot development in *Salix* is commonly sympodial; however, in the seedling stage and immediately following the first dormancy monopodial development has been observed (Sugaya, 1956a and 1956b). Monopodial growth was observed in *Salix glauca* seedlings from Churchill (see discussion of seed germination and seedling growth). The internode-length is usually greater in *S. glauca* than in *S. brachycarpa*, giving the shoots of the latter species a characteristic "fan-like" appearance. However, this is a variable feature that requires further study.

The annual shoots (branchlets) are usually clothed with a pubescence varying from a dense woolly mat in *Salix brachycarpa* ssp. *brachycarpa* to thinly pubescent or glabrescent in some *S. glauca*. The trichomes are lost in time and after 2 and 3 years the branches are usually glabrescent. The branchlets vary in color from light green to dark reddish-brown. The branches are usually reddish-brown or grayish, although in some they are yellowish or black. The older branches usually have a grey exfoliating epidermis. Branchlets may be pruinose, but observations of the pruinose condition are incomplete due to the dense pubescence on some stems and due to the loss of pruinosity during the drying of specimens.

Roots. The roots of the *Salix glauca* complex are woody structures often considerably branched, the main secondary branches running parallel to the surface of the ground a few inches beneath it. The depth of the roots is probably often controlled in arctic and subarctic regions by the depth at which permafrost occurs.

The possibility of vegetative shoots originating from the roots was investigated in the field. Both *Salix glauca* and *S. brachycarpa* were excavated at Churchill, Manitoba. An individual of *S. glauca* growing on the outcrop ridge was excavated until about 9 feet of roots were exposed, and an individual of *S. brachycarpa* was excavated, exposing three secondary roots of 5, 11, and 15 feet each. In neither case were root-shoots found to occur. On the Gaspé Peninsula a plant of *S. argyrocarpa* Anderss. growing in stream-gravels was also excavated with similar results.

Some species of *Salix*, including *S. interior* Rowlee and *S. exigua* Nutt., do have vegetative shoots sprouting from the roots and this question must be investigated separately for each species. In the species included in the present study, sprouts originate only from stems, most frequently from the base of the main shoot.

Leaves. The leaves of the *Salix glauca* complex are dorsiventral structures ranging in shape from oblanceolate to narrowly lanceolate through elliptical and obovate to oval or suborbicular in some forms of *S. glauca.* Leaf-shape is of general taxonomic importance in spite of its wide variation within populations. The leaf-base generally varies from round to obtuse to acute or attenuate, with one extreme form being cordate or subcordate. The apex similarly runs the gamut of variation from obtuse or rounded through acute or even apiculate in some instances. The general shape of the leaf-extremities depends somewhat on the shape of the leaf, with the broader leaves having rounded or obtuse extremities and the narrower leaves the more tapering extremities.

The leaves also vary in size and shape according to their position on the shoot. The lowermost leaves (proximal) are more or less modified in shape and pubescence and mature very rapidly, almost as soon as the shoot begins to elongate and the leaves unfold. In *Salix brachycarpa* ssp. *brachycarpa* (at Churchill) there are usually 3 to 4 such modified leaves which have parallel sides and a rounded apex and an obtuse or acute base. They lack, or have very scattered, pubescence on the upper leaf-surface even when enclosed in the bud. This is in marked contrast to the uppermost (distal) leaves which are completely clothed with a dense pubescence in the bud. In *S. glauca* (at Churchill) there are only 2 or sometimes 3 modified proximal leaves which are similar in shape to those of *S. brachycarpa*, but with an acute or apiculate apex. They have long straight trichomes on the lower leaf surface and lack vesture above; the distal leaves are generally sparsely pubescent on both surfaces.

The leaf-blade in the *Salix glauca* complex is always glaucous beneath and variously pubescent on both surfaces. The trichomes vary in length and degree of waviness. They originate as an outgrowth of a single modified epidermal cell and remain a single cell. The base of the trichome cell is surrounded by a radiating series of 4 to 6 modified epidermal cells (see figs. 3-3 and 4-8). There are no apparent taxonomic differences in this characteristic within the *S. glauca* complex.

In *Salix* the stomata are generally of the rubiaceous type, in which two subsidiary cells flank the stomatal pore parallel to the long axis (Metcalf and Chalk, 1959). However, variation in this pattern is common (see figs. 4-2, 4-3, and 4-9). Stomata are abundant in the abaxial (lower) epidermis and may or may not be present in the adaxial epidermis. The size of stomata varies with the species. The length of stomata in *S. brachycarpa* ranges from 17-22.5 micra and in *S. glauca* from 19.8-33.4 micra (see fig. 2). The importance of the presence or absence of stomata in the adaxial epidermis and stomatal size will be discussed below.

The leaf-margin is generally entire, although often the proximal leaves have small glandular teeth. In some cases even the distal leaves have small teeth near the base of the blade.

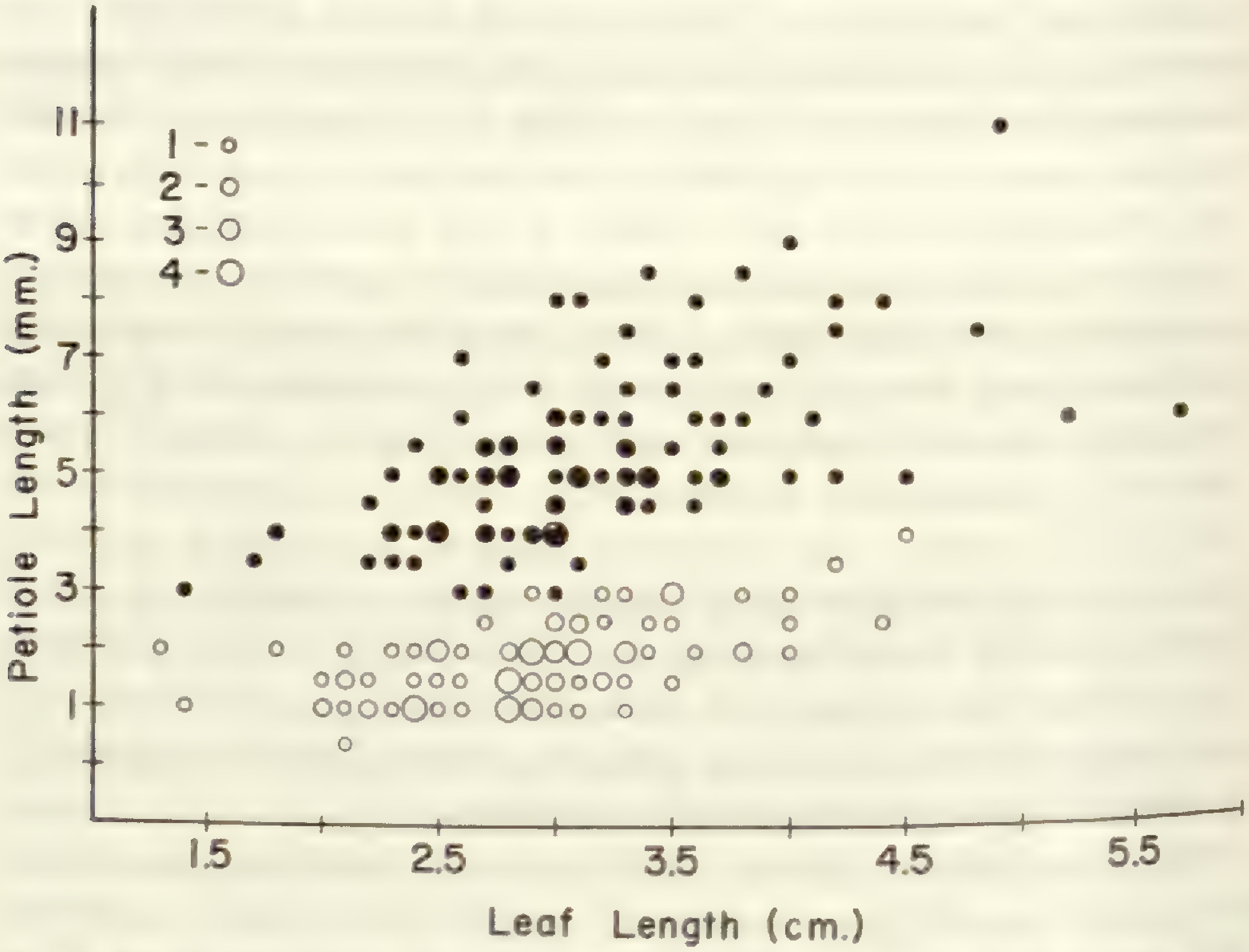


FIG. 1. A correlation of petiole-length and leaf-length in *Salix glauca* and *S. brachycarpa* at Churchill, Manitoba. The data were obtained from field local population samples of the species. The populations were located along the estuary of the Churchill River: *S. brachycarpa* (solid circles) occurs in the salt-marsh community and *S. glauca* (open circles) in the adjacent willow-shrub community. In this region, these taxa are readily distinguished on the basis of a correlation between petiole-length and leaf-length.

The leaves are always petiolate; however, in *Salix brachycarpa* the petiole may be very short. The length of the petiole is a relatively constant characteristic and is of taxonomic importance in the *S. glauca* complex. The correlation between petiole-length and leaf-length is shown in fig. 1. These characters are of diagnostic value in the species studied.

A pair of glandular-margined stipules flanks the base of the petiole. The stipules are usually prominent although variable in shape, and may be reduced to small glandular processes. Their shape and size vary in different species and in relation to the vigor of the shoot. The time of abscission of the stipule has been regarded by Raup (1959) to be of diagnostic importance, and *Salix glauca* var. *perstipula* was characterized by stipules persistent for several years. I have not yet studied this characteristic exhaustively, but I suspect that stipule-persistence is often related to the environment and is of limited taxonomic value.

Distribution of Stomata. In *Salix* stomata always occur in the abaxial leaf-epidermis. However, in some species or groups of species, stomata also occur in the adaxial epidermis, and a study of the distribution of stomata is primarily concerned with this variation. When stomata do occur in the adaxial epidermis they may be either distributed generally over the surface or localized at the extreme apex. Adaxial stomata are characteristically larger and more widely spaced than abaxial stomata.

Sectional importance was attributed to the distribution of stomata by A. and E. Camus (1904), and they described it as a fixed characteristic. It was used by these authors as the primary dichotomy in their anatomical key to the sections of *Salix* of Europe. Their section *Frigidae* (which included *S. glauca*) was described as lacking adaxial stomata.

During the years in which Schneider studied the *Salix* of North America (ca. 1918-1921) he paid particular attention to this character, as his annotations on herbarium-specimens and his comments in the literature testify (Schneider, 1918a, 1918b, and 1919). However, he found extensive intrasectional variation in the distribution of stomata and reduced the use of it from sectional to specific application. Schneider (1918b) utilized the distribution of stomata to distinguish some closely related species, e.g. *S. brachycarpa* from *S.*

pseudolapponum (= Rocky Mt. phase of *S. glauca*). He did note the occurrence of intraspecific variation but he did not elaborate upon it. Since Schneider's work, no taxonomic use has been made of stomatal distribution in *Salix,* although both M. L. Fernald and H. M. Raup considered it and found it to be undependable (Raup, pers. comm.).

In this examination of the taxonomic value of stomatal distribution a preliminary survey of 8 taxa has been made, and two possible sources of error are considered. Three of the eight taxa, *Salix chlorolepis* Fern., *S. arctica,* and *S. arctophila,* are not members of the *S. glauca* complex but they are closely related and may at times be involved in hybridization with members of the complex.

The results of this preliminary survey are presented in Table I. In each specimen the largest distal leaf on a shoot was examined and the distribution of adaxial stomata noted. The following classes of stomatal distribution in the adaxial epidermis were recognized: 1) adaxial stomata absent, 2) adaxial stomata present at the extreme apex, and 3) adaxial stomata present (i.e. generally distributed over the surface).

TABLE I. DISTRIBUTION OF STOMATA

Taxon	Number of specimens	Adaxial stomata[1]		
		Absent	Apex only	Present
S. brachycarpa ssp. *brachycarpa*	19	10	7	2[2]
ssp. *niphoclada* var. *niphoclada*	3	2	1	0
var. *fullertonensis*	4	0	1	3
S. brachycarpa ssp. *brachycarpa* × *S. chlorolepis*	7	1	3	3
S. chlorolepis	4	0	3	1
S. glauca (Europe and Asia)	7	3	4	0
(North America)[3]	38	26	12	0
(Colorado and Wyoming)	5	0	1	4
S. arctica	11	0	0	11
S. arctophila	2	1	1	0

[1] All specimens have stomata in the abaxial epidermis.

[2] Specimens from Mt. Albert, Quebec.

[3] Excluding specimens from Colorado and Wyoming.

The presence of a few adaxial stomata at the extreme apex of the leaf is part of individual variation occurring in species which otherwise lack adaxial stomata on mature leaves. In this preliminary survey, specimens having adaxial stomata at the apex (class 2) are tabulated separately, but in the discussion they are grouped with either class 1 or class 3, whichever is the predominant type in that taxon.

An examination of Table I reveals that, although there is considerable intraspecific variation in stomatal distribution, two general groups of species can be recognized. One, those lacking adaxial stomata, and two, those having adaxial stomata. Both groups include some individuals with adaxial stomata localized at the extreme apex. In general the *Salix glauca* complex is characterized by the absence of adaxial stomata, and *S. arctica* is characterized by the presence of adaxial stomata. However, *Salix brachycarpa* ssp. *niphoclada* var. *fullertonensis* and the Rocky Mt. phase of *S. glauca* possess adaxial stomata and *S. arctophila*, sometimes considered conspecific with *S. arctica* (Drury, 1962), lacks adaxial stomata.

Although general patterns are suggested and exceptions to these patterns can be observed, general taxonomic use of the characteristic is not warranted until two important sources of error, individual variation and environmental variation, are considered.

Individual variation. The correlation of the distribution of stomata and the developmental position of leaves on the annual shoot was studied in two species. The leaves from three shoots of *Salix brachycarpa* ssp. *brachycarpa* (*Argus 499-58*, Churchill, Manitoba) and *S. glauca* (*Argus 518-58*, Churchill, Manitoba) were removed, numbered successively from the base, cleared, and stained. Each leaf was examined for the distribution of adaxial stomata. The following is a summary of the data obtained: *Salix brachycarpa* — leaves 1, 2, and 3, adaxial stomata present; leaf 4, adaxial stomata at extreme apex; leaves 5 through 8, adaxial stomata absent. *Salix glauca* — leaves 1 and 2, adaxial stomata present; leaves 3 through 5, adaxial stomata at extreme apex; leaf 6, adaxial stomata absent.

Although both of these taxa are generally characterized by an absence of adaxial stomata they may sometimes have a few adaxial stomata at the leaf-apex. The 2 or 3 proximal leaves which have been observed to have adaxial stomata are modified in shape and size from the distal leaves and would not ordinarily be selected for use in a taxonomic study. However, this individual variation does emphasize the importance of using comparable organs and points out that the generalization that these taxa lack adaxial stomata is true only in reference to the distal leaves on the shoot. This variation may also explain the tabulation of some specimens of these taxa as having adaxial stomata at the leaf-apex. The leaves studied may have been selected from the intermediate zone between the proximal and the terminal leaves in which adaxial stomata are usually found to occur at the leaf-apex.

Environmental Variation. It was noted by A. and E. Camus (1904) that the distribution of stomata in the leaves of *Salix* varied in different habitats. However, the nature and extent of this variation was not discussed. Three cases can be cited in which different stomatal distribution patterns are apparently correlated wth environmental differences. In each case a comparison is made between leaves from the same individual under natural field-conditions and under cultivation at Jamaica Plain, Massachusetts.

1) *Salix glauca* (*Argus 501-58*, Churchill, Manitoba). Field: adaxial stomata at apex. Cultivated: adaxial stomata absent.

2) *Salix glauca* (*Levi 3*, Gothic, Colorado) Rocky Mt. phase. Field: adaxial stomata present. Cultivated: adaxial stomata absent.

3) *Salix chlorolepis* (*Argus 84-59*, Mt. Albert, Quebec). Field: adaxial stomata present. Cultivated: adaxial stomata at apex.

In each case adaxial stomata are absent or of more restricted distribution under cultivation than under natural field-conditions. More examples can be cited in which no difference is apparent between specimens under cultivated or field conditions, but, nevertheless, the occurrence of this variation is provocative. It is possible that the variation in stomatal distribution is not related to differences in environment, but to leaves originating from cuttings. However, in each case the shoots on which the leaves were borne were not adventitious, but produced from axillary buds. Although these data are not conclusive they do support the observations of A. and E. Camus (1904) suggesting that environmental influence on stomatal distribution may provide a source of error.

It is doubtful if sections, as presently understood, can be characterized by stomatal distribution. However, the intrageneric scope of this study is limited and an expanded survey may modify this conclusion. A recent paper by Watson (1962) in which the sectional importance of stomatal distribution in the *Epacridaceae* was established should prompt an extensive survey of *Salix*. The specific differences with respect to this character are inadequately understood and presently are of little or no taxonomic value.

Stomatal Length. The length of stomata in *Salix* was reported by A. and E. Camus (1904) to vary with the species, and even a cursory comparison of representative epidermal sections will corroborate this (compare figs. 3 and 4). The possibility that variation in stomatal length may be correlated with chromosome-number (see section on Cytology) enhances the potential significance of this characteristic and justifies a detailed consideration of it (see section on Techniques).

The length of stomata was determined for five species and the means and total ranges are presented in fig. 2. These taxa are the same as were considered in the section on stomatal distribution; only two, *Salix brachycarpa* and *S. glauca*, are members of the *S. glauca* complex.

The length of stomata in the three infraspecific taxa of *Salix brachycarpa* is essentially the same, with a mean varying from 19.6 to 20.6 micra. *Salix brachycarpa* ssp. *niphoclada* var. *fullertonensis* is an exception in this characteristic, as in others, and there is a strong suggestion that two stomatal lengths are represented in this taxon, one within the range of *S. brachycarpa* ssp. *brachycarpa* and the other within the range of *S. glauca*. For this reason, two means are given for this taxon.

Stomatal length-data for *Salix glauca* (fig. 2) are presented for 4 phases, plus an intermediate zone in North America, and the area Europe and Asia (see *Salix glauca*). Stomatal length varies from a mean of 26.3 micra in the Eastern phase to 30.1 micra in Europe and Asia. These mean lengths are in marked contrast to the report of stomata 8-15 micra long in European *S. glauca* by A. and E. Camus

(1904). Although an error by these authors may be suspected, it is possible that a form of this species with short stomata, similar to *S. brachycarpa,* occurs in Europe.

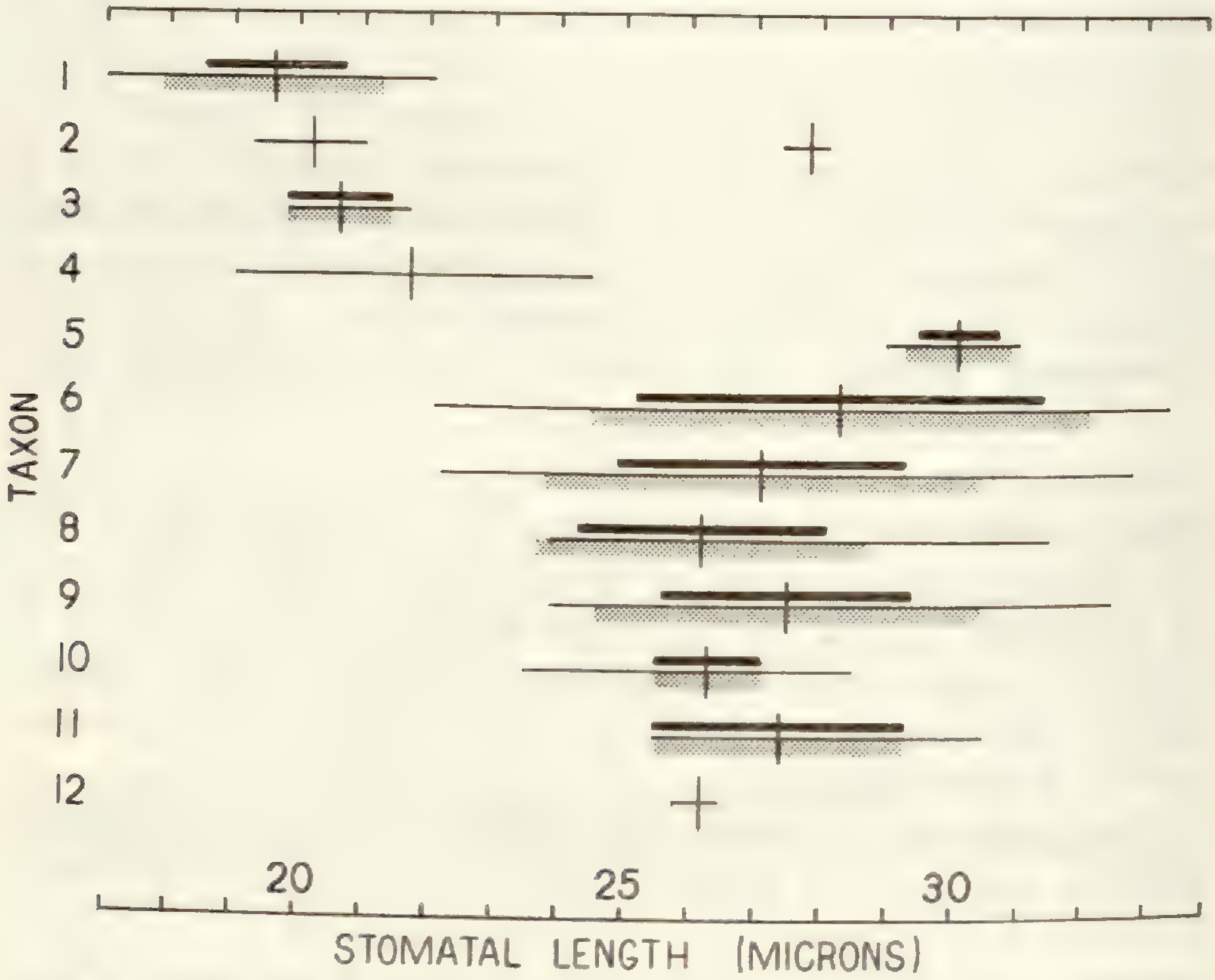


FIG. 2. Stomatal length of selected species of *Salix.* The mean, range, standard deviation, and two standard errors are presented as described in section Techniques. The sample size, in parentheses, follows each species. 1. *S. brachycarpa* ssp. *brachycarpa* (10); 2. *S. brachycarpa* ssp. *niphoclada* var. *fullertonensis* (4); 3. *S. brachycarpa* ssp. *niphoclada* (4); 4. *S. chlorolepis* (3); 5. *S. glauca,* Europe and Asia (8); 6. *S. glauca,* Beringia phase (6); 7. *S. glauca,* Western phase (11); 8. *S. glauca,* Northwest Territories (7); 9. *S. glauca,* Rocky Mt. phase (10); 10. *S. glauca,* Eastern phase (15); 11. *S. arctica* (5); 12. *S. arctophila* (2). See text for discussion.

The range of stomatal length measurements in *Salix glauca* is very great, from 22.1 to 33.4 micra, and tends to obscure any intraspecific differences. Nevertheless, a significant difference in the means of material of the Eastern phase in North America and of Europe and Asia is observed. These components of *S. glauca* can be distinguished on the basis of stomatal length.

The mean length of stomata in *Salix chlorolepis* is 21.0 micra (within the range of *S. brachycarpa*). The mean length of stomata for *S. arctica* is 27.4 micra and for *S. arctophila* is 26.2 micra. Stomatal length in these taxa falls within the range of *S. glauca.*

Camera lucida drawings of representative epidermal sections for four species are illustrated in figs. 3 and 4. The possible correlation of stomatal length and chromosome-number is discussed below (see section Cytology).

Environmental Inflence on Stomatal Length. To examine the possibility that the environment, which often has a

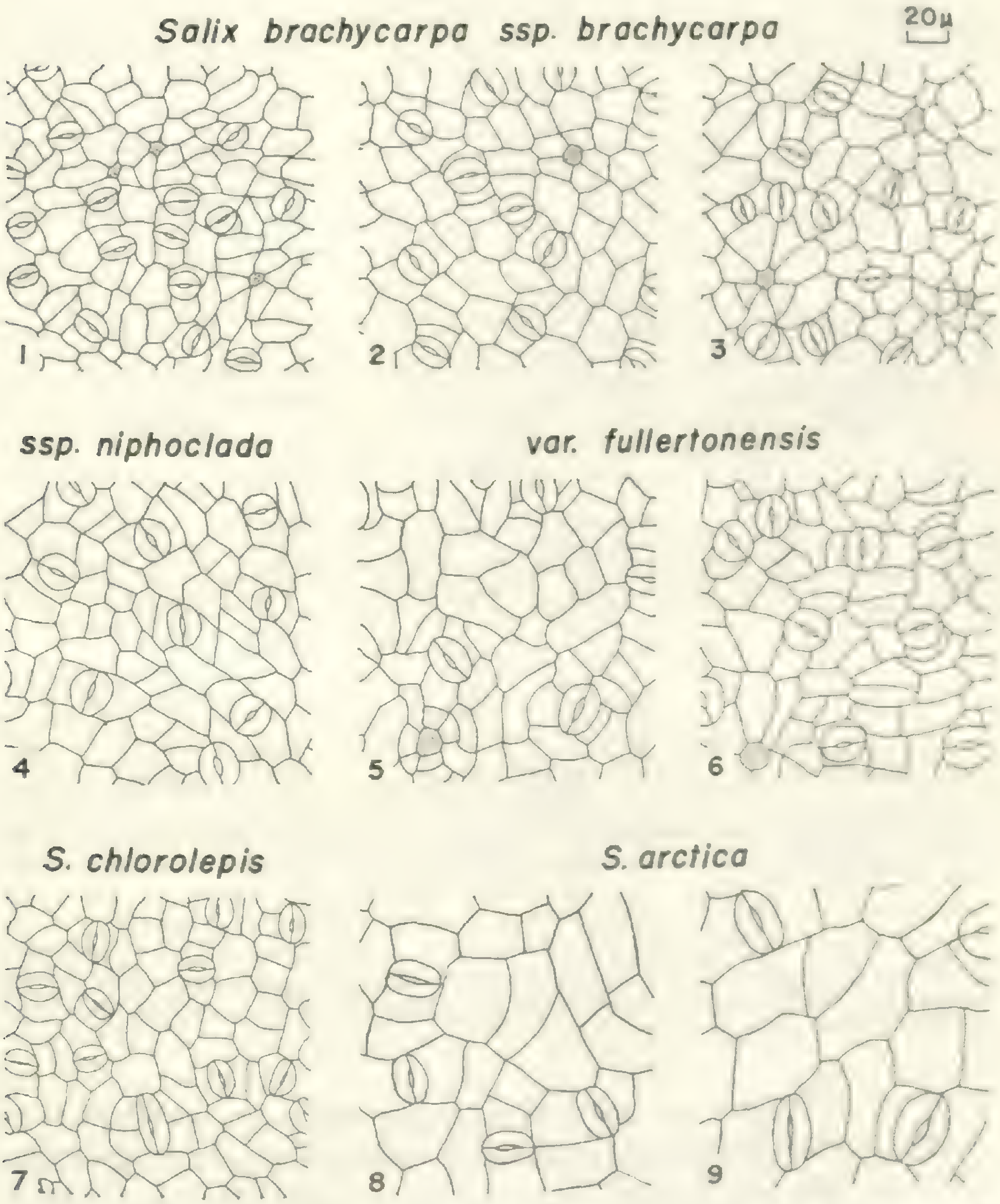


FIG. 3. Representative sections of the abaxial epidermis of *Salix brachycarpa*, *S. chlorolepis*, and *S. arctica*. 1-3. *S. brachycarpa* ssp. *brachycarpa*. 1. *Weber [illegible]*, North Saskatchewan R., Alberta. 2. *Argus [illegible]*, Churchill, Manitoba. 3. *Shear and Bessey 4002*, Higho, Colorado. 4. *S. brachycarpa* ssp. *niphoclada*. *Johnson, Viereck, and Melchior 673*, Kukpuk R., Alaska. 5-6. *S. brachycarpa* ssp. *niphoclada* var. *fullertonensis*. 5. *Porsild 17270*, Victoria Isl., N.W.T. 6. *Malte [illegible]*, Chesterfield Inlet, N.W.T. 7. *S. chlorolepis*, *Fernald [illegible]*, Mt. Albert, Quebec. 8-9. *S. arctica*. 8. *Argus 82-59*, Mt. Albert, Quebec. 9. *Heusser 4T*, Tulsequah Lake, British Columbia. Stippled cells are trichomes. The drawings were made using a camera lucida.

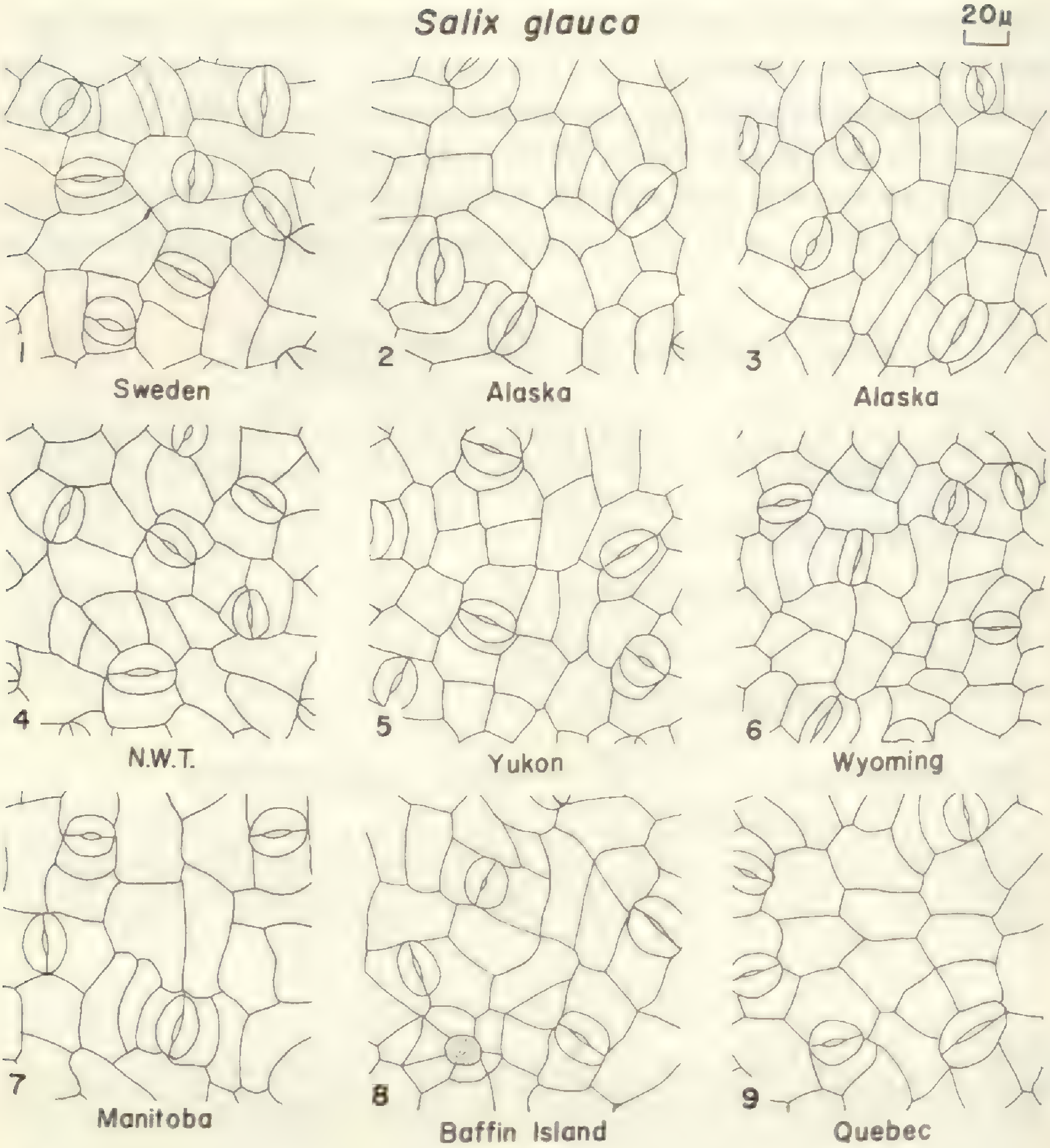


FIG. 4. Representative sections of the abaxial epidermis of *Salix glauca*. 1. *Asplund*, 27 July 1949, Lapland, Sweden. 2. *Johnson, Viereck, and Melchior* 303, Ogotoruk Cr., Alaska. 3. *Argus 1145*, Phelan Cr., Alaska Range, Alaska. 4. *Lewis 842*, Great Slave Lake, N.W.T. 5. *Raup and Correll 11061*, Watson Lake, Yukon. 6. *J. and M. Reed 1668-69*, Medicine Bow Mts., Wyoming. 7. *Argus 340-58*, Churchill, Manitoba. 8. *Malte 118709*, Lake Harbor, Baffin Island. 9. *Victorin and Germain 18925*, Mingan Archipelago, Quebec. The stippled cells are trichomes. The drawings were made using a camera lucida.

marked influence on leaf size, may have an influence on stomatal size, material from seven specimens growing under natural field conditions was compared with the same individuals growing under cultivation at the Arnold Arboretum, Jamaica Plain, Massachusetts (fig. 5 and table II). For each specimen the relative leaf area of a representative leaf from each specimen was determined by leaf-length × leaf-width, and the mean stomatal length was based on ten measurements.

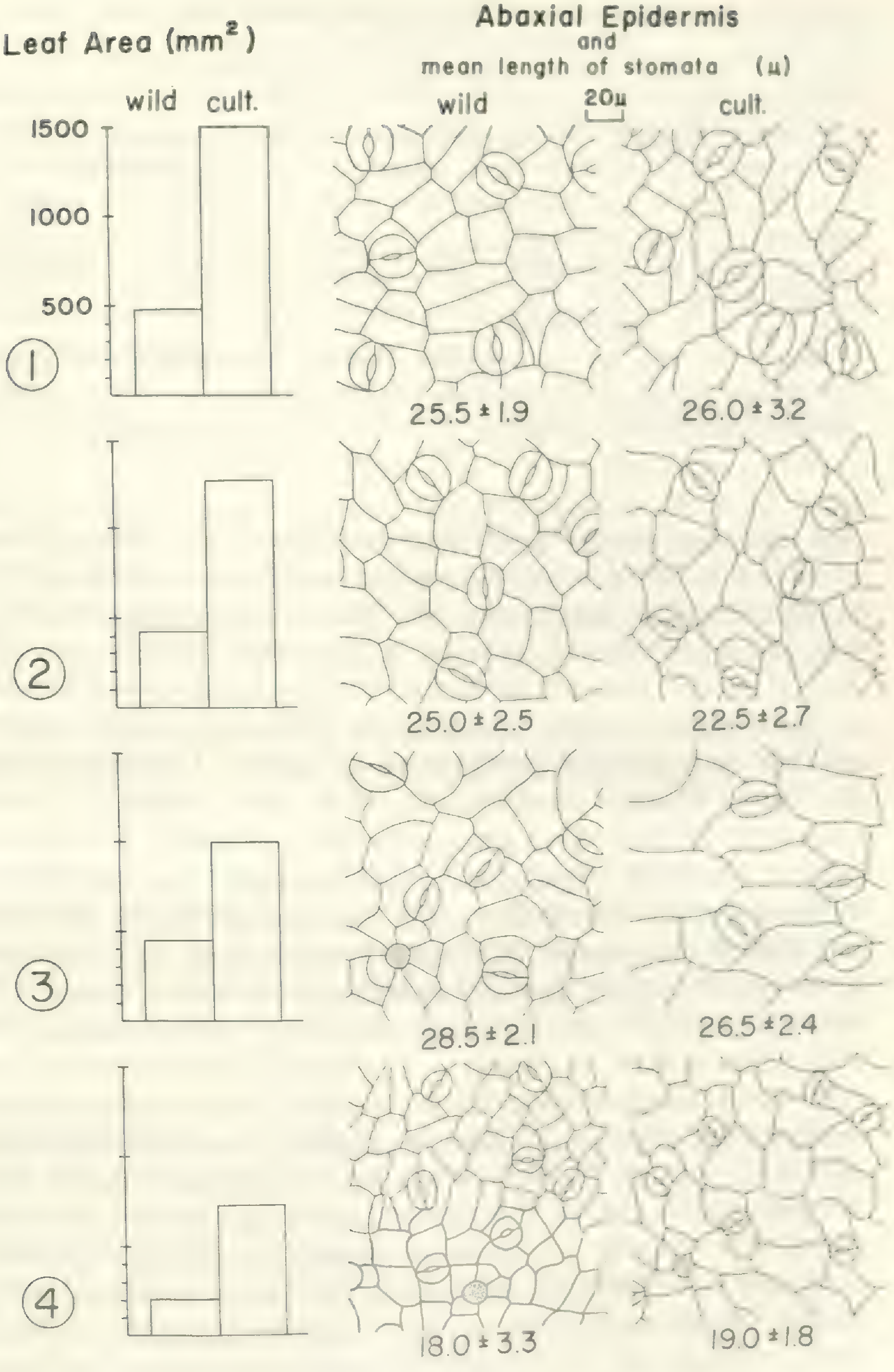


FIG. 5. Comparison of leaf-area and stomatal length under natural and cultivated conditions. Relative leaf-area is the product of leaf-length × leaf-width. The mean stomatal length and the standard deviation are given beneath the drawing of a representative section of the abaxial epidermis. 1. *Salix glauca*, *Argus* [illegible], Churchill, Manitoba. 2. *S. glauca*, *Argus* 516-[illegible], Churchill, Manitoba. 3. *S. glauca*, [illegible], Gothic, Colorado. 4. *S. brachycarpa* ssp. *brachycarpa*, *Argus 81-59*, Mt. Albert, Quebec. The drawings of epidermal sections were made using a camera lucida.

TABLE II. ADDITIONAL COMPARISONS OF LEAF-AREA AND STOMATAL LENGTH UNDER NATURAL AND CULTIVATED CONDITIONS

Taxon	Relative area of leaf (mm^2)		Stomata length (Microns)	
	Wild	Cult.	Wild	Cult.
Salix glauca, Rocky Mt. phase (*Levi 8,* Elk Mt., Colorado)	330	800	24.5±2.9	22.5±2.7
S. chlorolepis (*Argus 84-59,* Mt. Albert, Que.)	128	612	21.5±3.2	18.5±2.4
S. arctica (*Argus 82-59,* Mt. Albert, Que.)	330	1560	25.5±2.9	27.5±2.7

In two specimens of *Salix glauca* from Manitoba (figs. 5-1 and 5-2) the leaf-area was increased about three times in the cultivated specimens, but this was accompanied neither by a significant change in stomatal length nor by change in the size of epidermal cells. Leaf enlargement, in these cases, is due primarily to increased cell-divisions and not to a marked increase in cell-size. In material of *S. glauca* from Colorado (fig. 5-3 and table II) leaf area is about two times greater in the cultivated specimens than in the field collections. In these cases the epidermal cells are greatly increased in size, indicating that the greater leaf-area is due to cell enlargement as well as cell-division. However, the mean stomatal length remains unchanged. A representative of *S. brachycarpa* ssp. *brachycarpa* (fig. 5-4) also showed a marked increase in leaf-area under cultivation which, although accompanied by a small increase in epidermal cell-size, showed no change in stomatal length. The leaf area of *S. chlorolepis* and *S. arctica* (table II) was increased almost five times under cultivation, but no significant change in stomatal length could be detected.

It can be concluded that favorable environmental conditions which apparently elicit a marked increase in leaf-area, both through increased cell-divisions and cell enlargement, do not result in a significant change in stomatal length. This evidence is very important for it permits a greater confidence in the use of stomatal length particularly in wide ranging taxa which occupy a variety of habitats.

Seed Germination and Seedling Development. If provided with a suitable environment, seeds will begin to germinate within 12 to 24 hours. Within 48 hours 90 to 100 per cent germination may take place. The length of seed-viability is generally regarded to be only a few days, but under the proper conditions *Salix* seeds may remain viable for 9 to 10 months. Several authors including Toepffer (1915) and Sugaya (1956a) note that seeds may persist through the winter and germinate the following spring. This has also been observed in *S. glauca* where most of the seeds germinate in the year they are produced, but some may overwinter and germinate the following spring (Söyrinki, 1939). Seeds of *S. glauca* from Churchill, Manitoba, showed some ability to germinate after storage for 20 days under warm dry conditions. Fresh seeds of *S. calcicola* and *S. planifolia* at Churchill placed on wet filter paper in a petri dish showed 90-100 per cent germination in 3-4 days. The per cent germination decreased with storage under warm, dry conditions.

During the first 24 hours of germination the seeds of *Salix glauca* assume a bowed position resting on the radicle and the tips of the cotyledons. Elongation of the hypocotyl continues, rupturing the seed coat. At this time a ring of hairs ("hypocotyledonary bush" of Reed (1955)) appears from the zone of brownish tissue located between the colorless radicle-cone and the yellow-green hypocotyl. The hairs in this ring are about 0.5 mm. long and may serve in anchorage and the absorption of water. The elongation of the now erect hypocotyl continues and radicle elongation is initiated. After 2 to 3 days the radicle is about 1.5 mm. long and root hairs are present along its length. The hypocotyl continues its elongation for about 7 days, at which time the cotyledons, having spread apart, reveal the beginning of epicotyl development.

After about 30 days, the seedling may be from 5-10 mm. long and bear 2-3 unfolded leaves. If the seedling is placed under "winter conditions" of short days and cool temperatures a terminal bud may be formed. This bud is formed by the clasping of the apical meristem by the two reddish-green subterminal leaves. The occurrence of an apical bud in *Salix* has been reported by Sugaya (1956a and 1956b) in seedlings of *Salix pauciflora* Koidzumi and in young shoots on cuttings of *S. reticulata* L. A terminal bud is ordinarily formed in *Salix* only during the seedling stage and at the time of its first dormancy.

REPRODUCTIVE MORPHOLOGY AND BIOLOGY

Inflorescence. The inflorescence of *Salix* is a highly reduced, simple, usually erect, unisexual structure called an ament or catkin. The species are dioecious, the individual plants bearing either staminate or pistillate aments. The relationship between the opening and development of the inflorescence and foliage buds is generally described using three terms: 1) *precocious,* inflorescence appearing before the foliage; 2) *coëtaneous,* inflorescence appearing at about the same time as the foliage; and 3) *serotinous,* inflorescence appearing after the foliage.

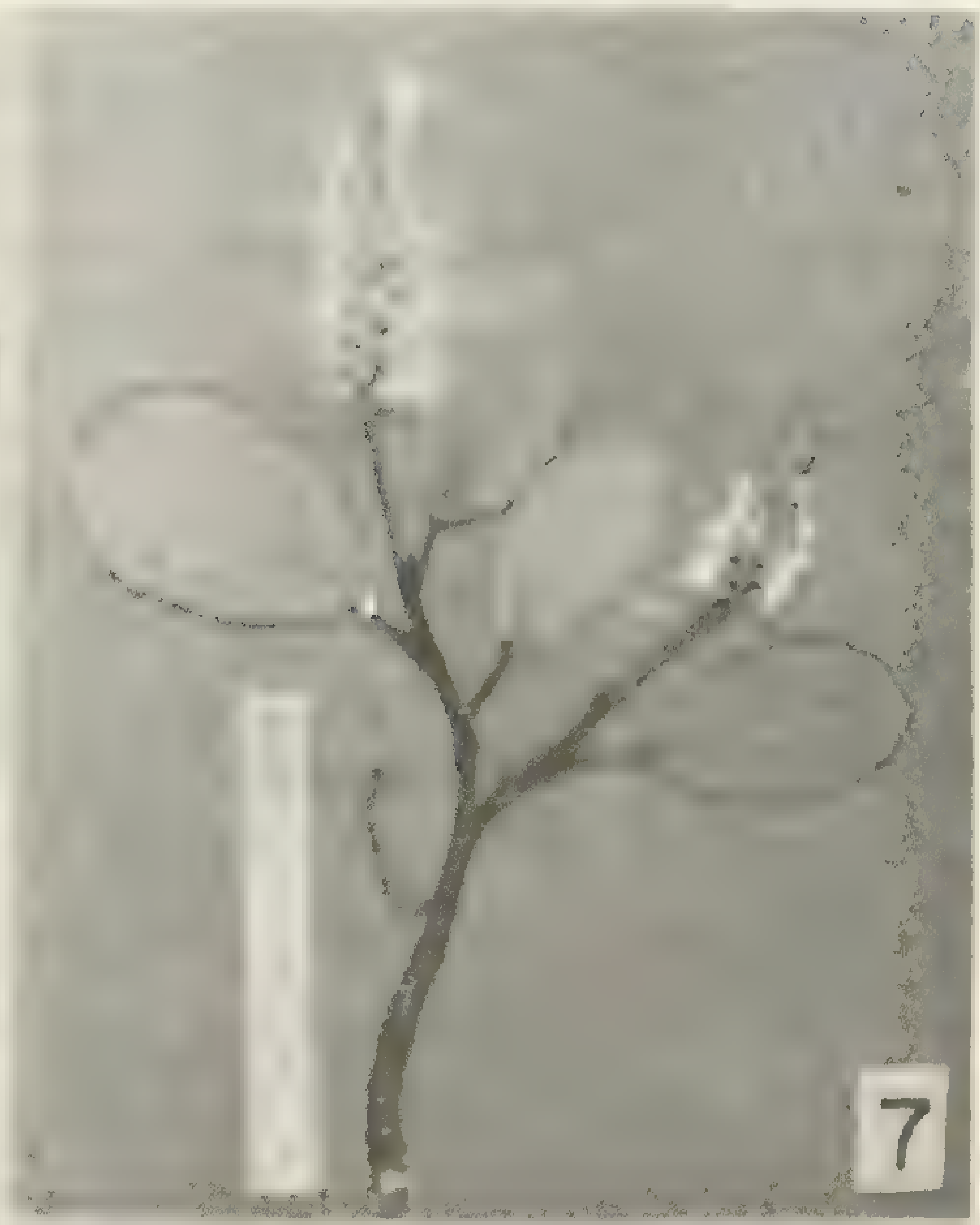
The pistillate aments are composed of pistillate flowers each consisting of a single pistil and its associated gland (s) borne in the axil of a bract. The staminate aments are composed of staminate flowers consisting of a variable number of stamens, two in the *Salix glauca* complex, and their associated glands borne in the axil of a bract. In the *S. glauca* complex the pistillate flowers have only one gland, rarely two, located adaxially, between the ovary and the rachis, and the staminate flowers have two glands, one located adaxially and the other abaxially.

The ament in the *Salix glauca* complex is always borne at the end of a reproductive shoot (Figs. 6 & 6a). This

FIGS. 6-8. Three general types of reproductive shoots in *Salix*. FIG. 6 and 6A. *Salix glauca* (*Argus 196-58*, 12 July 1958, Churchill, Manitoba). In *Salix glauca* the inflorescence develops about the same time as the vegetative shoots (coëtaneous) and they are borne several nodes below the branch apex. In pistillate individuals (illustrated) the aments (PA) are borne on long reproductive shoots (RS) bearing leaves similar to those at the proximal end of the vegetative shoots. The zone of abscission (A) is located between the distal leaf and the proximal flower. In staminate individuals the reproductive shoot may be shorter and bear small bract-like leaves. FIG. 7. ***Salix reticulata* (*Thieret and Reich 5818*, 30 July — 2 Aug. 1959, Horn Mts., N.W.T.).** **In *S. reticulata*** the reproductive buds are located subterminally and the reproductive shoots are long and prominent. In most individuals the vegetative shoots are absent and the reproductive shoots serve both vegetative and reproductive functions. FIG. 8. *Salix discolor* (*Argus 1-62-S* (left), 2 May 1962, Saskatoon, Sask., and *Argus 14-26* (right), 24 May 1962). In this and other precocious species, the inflorescence develops before the vegetative shoots appear and fruits may be formed before the vegetative shoots have matured (Fig. 8, right branch). In precocious species the reproductive shoots are very short or apparently absent and bear reduced bract-like leaves.

6

6a

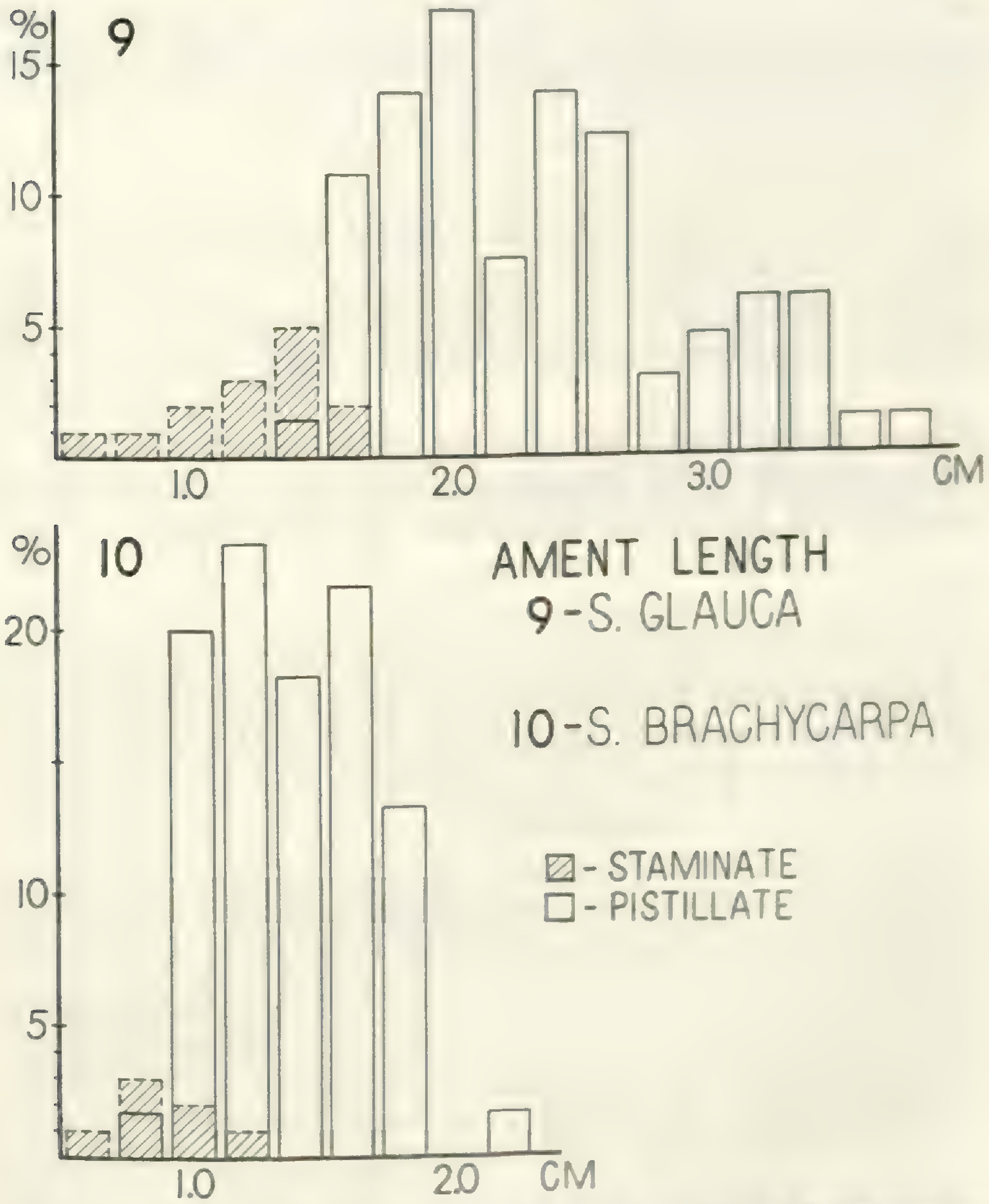


7

8

reproductive shoot is referred to in the literature as a peduncle and aments are described as "leafy-pedunculate" or "sessile". In some species such as *S. reticulata* the reproductive shoot is as prominent as the vegetative shoot and in these cases only the upper portion of the shoot above the leaves is called the "peduncle" and it is referred to as "a long leafless peduncle" (Fig. 7). Those species in which the reproductive shoot is very short or absent are the precocious flowering species such as *S. discolor* Muhl. and *S. planifolia* (Fig. 8). The "peduncle" terminology in common usage is unfortunate because it is inconsistent and inaccurate. Actually, the difference between the reproductive and the vegetative shoot is simply that the former is terminated by an ament. The internode between the last leaf on the reproductive shoot and the ament has a zone of abscission a variable distance above the last leaf. The region between this zone and the lowermost flower may be properly referred to as the peduncle and the region below it the reproductive shoot. In most cases, the ament is cut off by the abscission layer; however, at times the whole reproductive shoot may dry up and fall off. In *S. glauca* the staminate aments are borne on very short reproductive shoots and the aments are characteristically cut off above the last leaf. Since the shoot bearing the ament is not called a "peduncle" in this paper, there is no reason to refer to the leaves borne thereon as "bracts". This makes it possible to reserve this term for the structures subtending each of the flowers (*see* Bracts). The problem of the relationship between the ament, peduncle, and reproductive shoot requires detailed morphological and anatomical study.

In the *Salix glauca* complex the length of the pistillate aments has been considered to be of taxonomic value and taxonomists have characterized *Salix brachycarpa* as having shorter aments than *S. glauca*. Schneider (1919) noted that *S. brachycarpa* has pistillate aments varying from 1.5-2.5 cm. long in fruit, in contrast with the longer aments of *S. cordifolia* (eastern Canadian populations of *S. glauca*) which vary from 3.0-9.0 cm. long. When this generalization is analyzed in terms of local populations a wide range of variation is found. The length of fruiting pistillate aments was measured in two field local population samples from Churchill, Manitoba. *Salix glauca* (Fig. 9) ranges from 1.4-3.8 cm. long, and *S. brachycarpa* (Fig. 10) ranges from 0.7-1.9 (-2.2) cm. long. These data do not fully corroborate the observations of Schneider and illustrate the wide variation and overlap which may be encountered on the local population level. The variation described here applies only to populations in the Churchill, Manitoba

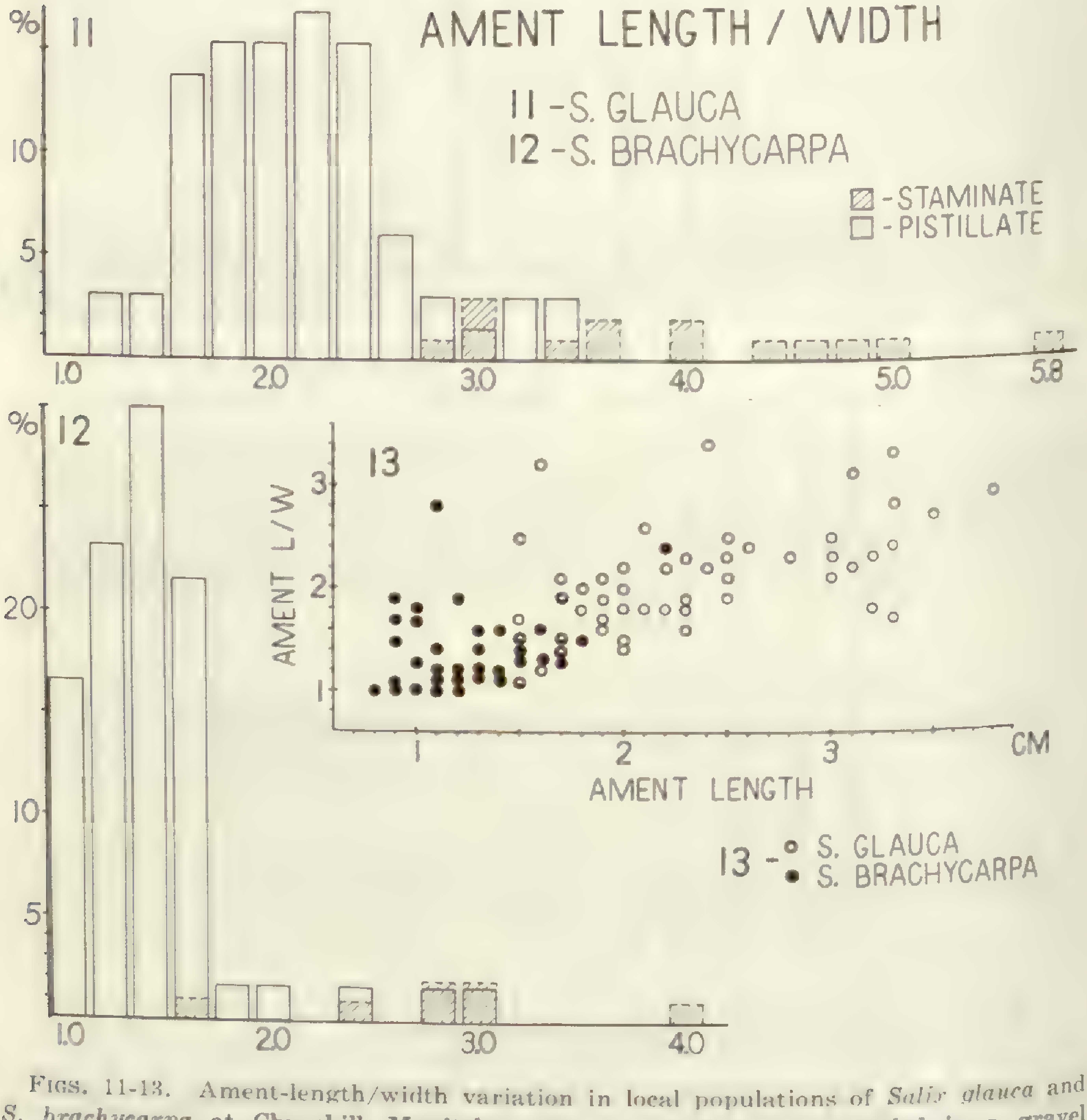


FIGS. 9 AND 10. Ament length variation in local populations of *Salix glauca* and *S. brachycarpa* sampled at Churchill, Manitoba. The data are based on field local population samples. *Salix glauca* (FIG. 9) was sampled in a gravel ridge habitat and *Salix brachycarpa* (FIG. 10) was sampled in a sand dune habitat. See text for discussion.

region. If populations of *S. glauca* from Alaska were compared with *S. brachycarpa*, overlap in pistillate ament length would be virtually absent and the characteristic would be of diagnostic value.

The staminate aments of both species in the Churchill, Manitoba region are short and their ranges almost coincide (Fig. 9 and 10). However, those of *S. brachycarpa* do show a tendency to be shorter.

The general shape of aments, particularly the pistillate, provides a more diagnostic characteristic than does ament-length when contrasting *Salix brachycarpa* and *S. glauca*. The pistillate aments of *S. brachycarpa* are often referred to as subglobose to oblong or short-oblong to spherical, in



FIGS. 11-13. Ament-length/width variation in local populations of *Salix glauca* and *S. brachycarpa* at Churchill, Manitoba. FIG. 11. *Salix glauca* sampled in a gravel ridge habitat. FIG. 12. *Salix brachycarpa* sampled in a sand dune habitat. FIG. 13. Correlation of pistillate ament-length and ament-length/width. The data are based on field local population samples. See text for discussion.

contrast to the cylindrical pistillate aments of *S. glauca*. An analysis of local population variation (Figs. 11 and 12) shows overlap almost as great as found in ament-length. However, a correlation of ament-length and ament-length/width provides a sounder basis for distinguishing these two species. (Fig. 13).

Bracts. The bracts of *Salix* are simple, entire structures subtending each flower, and have a vascular supply similar to that of normal leaves (Fisher, 1928). Fisher does not regard them as true bracts of the flower because their vascular supply is derived from the stele of the flower and not from the stele of the ament. She interprets them as pertaining to the flower and arising from the pedicel. Hjelmquist (1948) does not agree with this interpretation and cites examples of similar coalescence of bracts and flowers in other Amentiferae which in the case of *Salix* led to the vascular bundles becoming partly united. In the present paper, this structure is held to be a bract subtending the flower.

Variation in the size, shape, color, and pubescence of bracts is great even within a species. They vary in shape from narrowly linear to broadly oval. In the *Salix glauca* complex, certain bract shapes and sizes are superficially distinctive. For example, *S. brachycarpa* ssp. *brachycarpa* often has longer, broader bracts than does *S. glauca*; and linear bracts are common in *S. brachycarpa* ssp. *niphoclada*. A local population analysis of pistillate bracts (Figs. 14-2 and 15-2) reveals that although extremes may be distinctive, bract-shape and size are not of diagnostic value. Further, the staminate bracts (Figs. 14-1 and 15-1) are virtually identical in both *S. brachycarpa* and *S. glauca*. Although certain species seem to be characterized by bracts of a certain shape, this is a highly variable characteristic and of limited taxonomic use.

Bract color in *Salix* varies from yellow, tawny to green, black or bicolored (black at apex, light colored below). Bract-color has been used as an important characteristic at both the sectional and specific levels. Schneider (1918a) noted that color and pubescence of bracts afforded reliable criteria on which to distinguish section *Ovalifoliae* (the *S. arctica* complex) and section *Glaucae* (the *S. glauca* complex). The former with bracts ". . . usually more or less bicolor, being pale at base and dark brown, fuscous, or even blackish toward the apex . . ." and the latter with " . . . uniformly yellowish, light brown, or straw colored bracts." In general this characterization is accurate, but dark-brown to

FIGS. 14 AND 15. Bract-shape and size-variation in two local populations of *Salix glauca* and *S. brachycarpa* at Churchill, Manitoba. FIG. 14. *Salix glauca* (1) staminate bracts, (2) pistillate bracts. FIG. 15. *Salix brachycarpa* (1) staminate bracts (2) pistillate bracts. Illustration prepared using a microprojector. See text for discussion.

black bracts are observed in *S. glauca* in the southern Rocky Mountains and bicolored bracts occur in some material of *S. glauca* from Arctic Alaska.

Bract-color seems to vary with the ontogenetic stage of development of the flowers. Smith (1954) reported a color change in *Salix glauca* from Colorado (as *S. pseudolapponum*), from green to pinkish and finally to brown. A similar series of colors from green to yellow or light brown has been observed in *S. brachycarpa* at Churchill, Manitoba.

In 1905 Fernald used the green bracts of *Salix chlorolepis* to distinguish this taxon from *S. brachycarpa*. An analysis of a local population sample of *S. brachycarpa* from Mt. Albert, Quebec, where the endemic *S. chlorolepis* also occurs, shows a striking correlation between floral development and bract-color (Fig.16). Aments in anthesis have predominantly green bracts and those in postanthesis have yellow to tawny bracts. There is a continuous sequence of intermediate colors if ontogenetic processes and genetic differences between individuals are taken into account. The high frequency of green bracts in flowering specimens of *S. brachycarpa* brings into question the validity of the use of bract-color to distinguish it from *S. chlorolepis*.

The extensive occurrence of greenish bracts in *Salix brachycarpa* on Mt. Albert also may be related to its hybridization with *S. chlorolepis* (*see Salix brachycarpa* X *chlorolepis*). However, the occurrence of green bracts in *S. brachycarpa* at Churchill, Manitoba and the correlation between green bracts and the flowering stage in this taxon on Mt. Albert suggest that, although the green color may have been re-enforced in the Mt. Albert population, the correlation of bract-color and the stage of floral development is real and should be carefully considered.

Nectaries. The nectaries of *Salix* are usually small, flattened structures which secrete nectar from their apex. There may be one, two, or several associated with each flower. In the *S. glauca* complex one, or rarely two, is found in the pistillate flower and two in the staminate. If a single nectary is present it is located adaxially between the ament-axis or rachis and the sporophyll. If two are present, the second is located abaxially between the bract and the sporophyll. The abaxial gland is the smaller of the two. If more

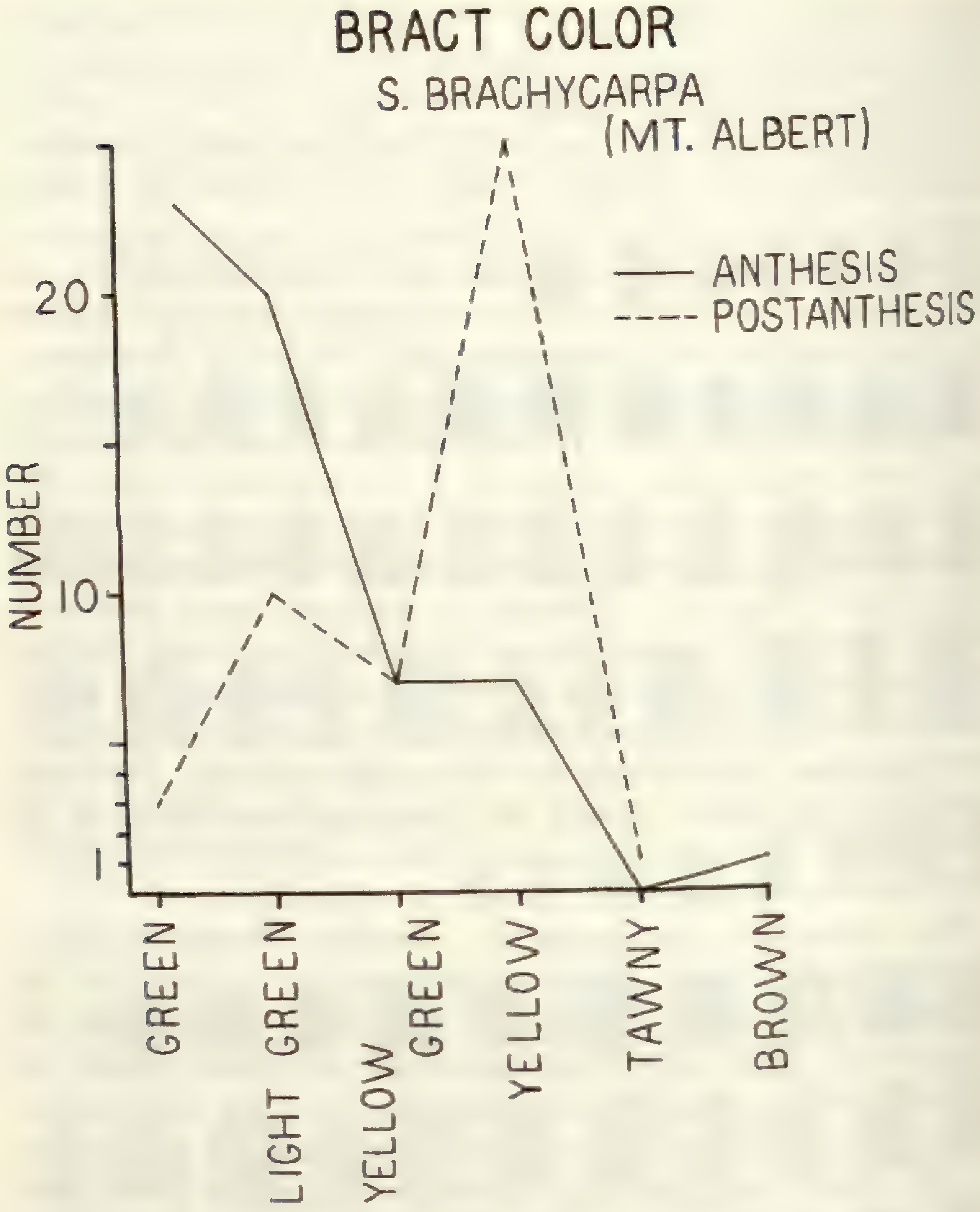


FIG. 16. Comparison of bract-color and stage of flowering in a local population of *Salix brachycarpa* from Mt. Albert, Quebec. See text for discussion.

glands are present they flank the sporophyll. In the *S. glauca* complex the adaxial gland varies in shape from long and tapering to short and broad; they are usually forked or lobed. Some of the variation in gland-shape and size is illustrated in Fig. 17. The variation in this structure has not been sufficiently studied to permit a clear evaluation of its taxonomic value, but it seems to be of limited usefulness in the species studied.

FIG. 17. Nectary-variation occurring in pistillate flowers of *Salix glauca* and *S. brachycarpa.* The nectaries illustrated in each figure were from a single individual. 1-3. *Salix glauca.* 1. *Argus 518-58,* Churchill, Manitoba. 2. *Argus 1148,* Phelan Cr., Alaska Range, Alaska 3. *Argus 379-58,* Churchill, Manitoba. 4-6. *S. brachycarpa* ssp. *brachycarpa.* 4. *Argus 498-58,* Churchill, Manitoba. 5. *Argus 412-58,* Churchill, Manitoba. 6. *Argus 416-58,* Churchill, Manitoba. 77 & 8. *S. brachycarpa* ssp. *niphoclada.* 7. *Viereck 1097,* Mt. McKinley Nat. Park, Alaska. 8. *Argus 629,* Mt. McKinley Nat. Park. 9. *S. brachycarpa* ssp. *niphoclada* × *glauca. Viereck 4805,* College, Alaska. The small nectaries to the right of the dash in 4, 5, and 9 are abaxial nectaries. Although second nectaries occupying this position are uncommon in pistillate flowers, three individuals having them are illustrated here. The abaxial glands are smaller and uncleft in contrast to the adaxial glands. The drawings were made using a micro-projector. The magnification is about 12X.

The use of the number of glands per flower as an important sectional characteristic, as was done by Schneider (1922), should be reexamined. He did not include *S. wolfii* in the same section as *S. glauca* because its staminate flowers have two glands. As we have seen, the staminate flowers of the species in the *S. glauca* complex also have two glands, although the pistillate flowers usually have only one. The difference which was supposed to exist between these two species does not in fact exist. Gland number appears to be somewhat variable and should be used with caution.

Stamens. The stamens vary in number in *Salix* with the diandrous group having one or two per flower and the pleiandrous group having a larger number, usually five. The filaments are commonly free although they may be more or less united toward the base. In the *Salix glauca* complex this is variable and stamens with free or united filaments may be found in a single specimen. A pubescence of long simple trichomes may be found near the base of the filaments. Each stamen is supplied with a single vascular trace (Fisher, 1928). The anthers dehisce by a longitudinal split between the two pollen-locules.

Pistil. The pistil is a flask-shaped structure which may or may not be pedicellate. In the *Salix glauca* complex both pedicellate (*S. glauca*) and non-pedicellate or sessile (*S. brachycarpa*) pistils occur. The length of the pedicel provides a reliable diagnostic feature to distinguish *S. glauca* from *S. brachycarpa.* In comparing field local population samples of these taxa from Churchill, Manitoba, *S. brachycarpa* was found to have a pedicel-length of 0.0 to 0.25 mm. in 80 per cent of the population and *S. glauca* a length of 1.0-2.0 mm. in 90 per cent of the population. An overlap of less than 10 per cent was found in the 0.5-1.0 mm. range.

The pistil may be glabrous or pubescent; in the taxa studied pubescent pistils are the rule with some becoming glabrate in age. The carpels are two in number and are united to form a unilocular ovary. They were considered by Rainio (1926) to be median with median placentae. However, this view is not generally accepted and Velenovsky (1904), Fisher (1928), and Hjelmquist (1948) all agree that the carpels should be interpreted as being transverse with the placentae formed at their edges. Fisher reports that each pistil receives six bundles and that the ventral ones are fused into two large placental bundles. The placentae are parietal, each bearing several erect, anatropous ovules (Hjelmquist, 1948).

A single style is present in all the taxa considered in the present study, although in some it is very short. In *Salix glauca* it varies from entire to bifurcate. The stigmas in the *S. glauca* complex are mostly four-lobed with each lobe more or less linear. In some cases the lobes may be short and only two in number.

Fruits and Seeds. The fruit of *Salix* is a capsule with loculicidal dehiscence. At the time of dehiscence the enclosed seeds are exposed revealing a coma of white or sometimes yellowish trichomes produced as outgrowths of the placentae (Takeda, 1936). At fruit maturity, the stigmas and often the styles drop off; the distal end of the capsule splits and the two halves curve backward. This releases the seeds which are small, exalbuminous, and provided with a coma attached loosely to their bases. The seeds are generally ellipsoidal to cylindrical and vary in length, depending somewhat on the species. In the *S. glauca* complex they vary from 1 to 2 mm. long. Toepffer (1915) reports the range of color within the genus to be from black to brownish or greenish. In the material I have examined the seed-coat is colorless and translucent, and any color that the seed possesses depends on the enclosed embryo. Viable seeds, and even some that are not viable, are generally greenish. However, when studied on herbarium specimens brownish or blackish seeds may be noted. The coma consists of trichomes often two or more times the length of the seed. In the species studied, trichomes four to seven times as long as the seed are not uncommon. The trichomes are fused at their proximal end into a ring that is loosely attached to the seed. The coma provides a "parachute" for each seed presumably greatly facilitating its dispersal.

Pollen. The *Salix* pollen-grain is generally prolate, tricolpate, intectate, and reticulate. The colpus is usually boat-shaped and it is usually regarded as lacking a germ pore. The reticulum is formed ". . . by isolated granules, columellae, standing on a continuous endexine." (Faegri, 1953). The columellae are not fused into a continuous tectum and the grains are intectate. The upper parts of the columellae are fused into a "reticulum tectum" (Faegri, 1953). The grains range in size from 20-24 microns in some small grains, to 33-36 microns in larger ones (Erdtman, 1952). The size seems to be related to the chromosome-number but Erdtman cautions against making any assumptions based on this information.

The pollen-grains are extremely variable in size, shape, number of colpi, pattern of sculpturing, etc. (Straka, 1950; Faegri, 1953). The degree of variation which had been noted by Høeg (1929), and Erdtman's (1952) cautioning against relating grain-size and ploidy-level suggest that the use of pollen-grains as a taxonomic character should be avoided or used with extreme caution. I have seen two attempts to distinguish certain species on the basis of pollen-grain morphology. These were by Straka (1950) and Faegri (1953). For a non-palynologist the keys presented by these authors are of limited value. Faegri points out that "... the morphological details of the *Salix* pollen grain are so difficult to observe and interpret, being in fact of the same order of magnitude as the maximum resolution power of the visible light microscope, that only the very best optic equipment is adequate for the task." The species which Straka was able to distinguish on the basis of their pollen-grain morphology were *S. glabra, S. silesiaca, S. herbacea, S. daphnoides, S. pentandra,* and *S. alba.* Faegri provided a key to distinguish *S. herbacea, S. myrsinites, S. m.* ssp. *weigliana, S. polaris, S. glauca, S. glandulifera, S. lapponum, S. reticulata,* and *S. lanata.*

A study of six hybrid species by Straka (1950) showed their grain type to be dominated by one parental type, malformations to be frequent, and new combinations rare. This suggests that hybrids could be distinguished on the basis of malformed pollen-grains. I have not been able to detect such grains in any of the hybrids I have examined. To my knowledge, this characteristic has not been used taxonomically, but it deserves some attention.

Pollination. *Salix* is generally regarded to be insect-pollinated, although considerable quantities of pollen may be found to be transported by wind. Høeg (1929) in his report on the pollen-grains carried by two species of *Bombus* on Ellesmere Land found that *Salix* grains were most commonly carried. Insects are frequent visitors of *Salix* and the presence of nectaries suggests that the flowers are largely adapted to an entomophilous mode of pollination. Knuth (1909) noted, ". . . as insect visitors go from one species of willow to another indiscriminately, it is difficult to assign them insects to individual species." However, the importance of wind-pollination cannot be overlooked, especially in the northern regions where strong winds often prevail in summer. The relative importance of these two means of pollen-transfer is of particular importance in estimating population size in this genus. At any rate the pollination is promiscuous, no matter which agent is at work, and hybridization resulting from this non-specific transfer of pollen is probably common.

Phenology. The relationship between the opening and development of the inflorescence and the foliage (*see* Inflorescence) is also reflected in the time of flowering of the species. Precocious species flower early in the season and the coëtaneous and serotinous species late in the season. During 1958, seasonal notes were made at Churchill, Manitoba, on the phenology of most species of *Salix* in the area; the flowering time data are presented in Fig. 18. The data are based in part on casual observations and in part on successive collections, and represent the dates of anthesis of the species studied. There will be variation in flowering time from year to year but the flowering sequence can be expected to remain relatively constant. Some of the species plotted, such as *S. vestita*, *S. bebbiana*, and *S. alaxensis*, were observed only rarely and their flowering period should be regarded as only approximate.

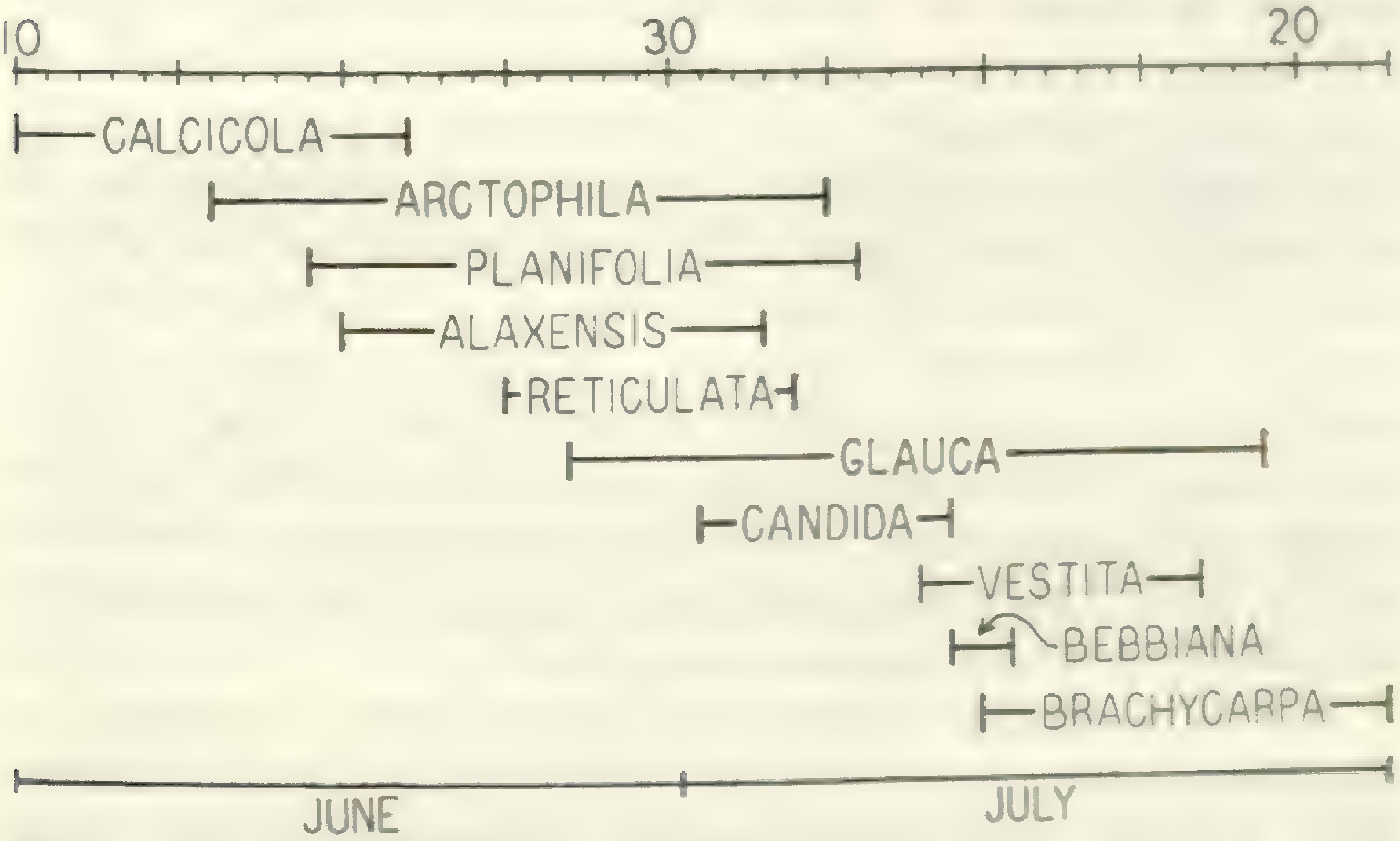


Fig. 18. **Comparative flowering time of the species of *Salix* occurring at Churchill, Manitoba.** The data are based on field-observations made during June and July 1958. **See text for discussion.**

A general pattern of variation in flowering time can be noted, with the precocious species *Salix calcicola* and *S. planifolia* flowering early, and those coëtaneous species, such as *S. glauca* and *S. brachycarpa*, flowering later. This pattern is supplemented by characteristics related to the adaptation of some species to a short arctic growing season. *S. arctophila* and *S. reticulata* are examples of arctic-alpine species which flower early although they are coëtaneous. *S. bebbiana* and *S. brachycarpa* are examples of boreal species which are coëtaneous and flower late in the season.

The spread in time of flowering of the *Salix* species at Churchill may represent an isolating mechanism which reduces the degree of hybridization between these species. *Salix glauca* and *S. brachycarpa* are probably significantly isolated by this mechanism. Further detailed phenological information from various localities would be of particular interest in studies of hybridization and evolution in *Salix*.

Cytology. Polyploidy is important in the evolution of *Salix* and a knowledge of the chromosome levels in the *Salix glauca* complex is essential to an eventual understanding of its evolution. Unfortunately, only a few counts are available for species in this complex and these are inadequately documented by herbarium vouchers. During the course of this study some chromosome counts were made. However, due to a series of difficulties the counts are too few and the results not unequivocal. In spite of limitations, these data are of some value and contribute to our understanding of polyploidy in the *S. glauca* complex.

The chromosome counts that have been reported for European *Salix glauca* indicate that this species is octoploid with two basic numbers, 22 and 19. Material having a basic number of 19 (2n = 152) is reported by Marklund Floderus (1931), and Löve and Löve (1948), and material with a basic number of 22 (2n = 176) is reported by Wilkinson (1944). The 22 number is believed by Wilkinson to be due to the fragmentation of chromosomes in the 19 base type. A second "species", *S. callicarpaea* (eastern Canadian populations of *S. glauca*), has been reported to be decaploid (2n = 190) by Löve (1954).

Counts based on *Salix glauca* and *S. brachycarpa* from Churchill, Manitoba, and on *S. brachycarpa* ssp. *brachy-*

carpa × *glauca* from the Medicine Bow Mts., Wyoming are reported for the first time in this study. Since completely accurate counts proved to be difficult to make, the numbers of chromosomes actually counted are presented here with no attempt to adjust them to their probable ploidy level. See section on Techniques for a discussion of methods.

The results are presented in Table III and in Fig. 19. Several interesting features of these data should be noted.

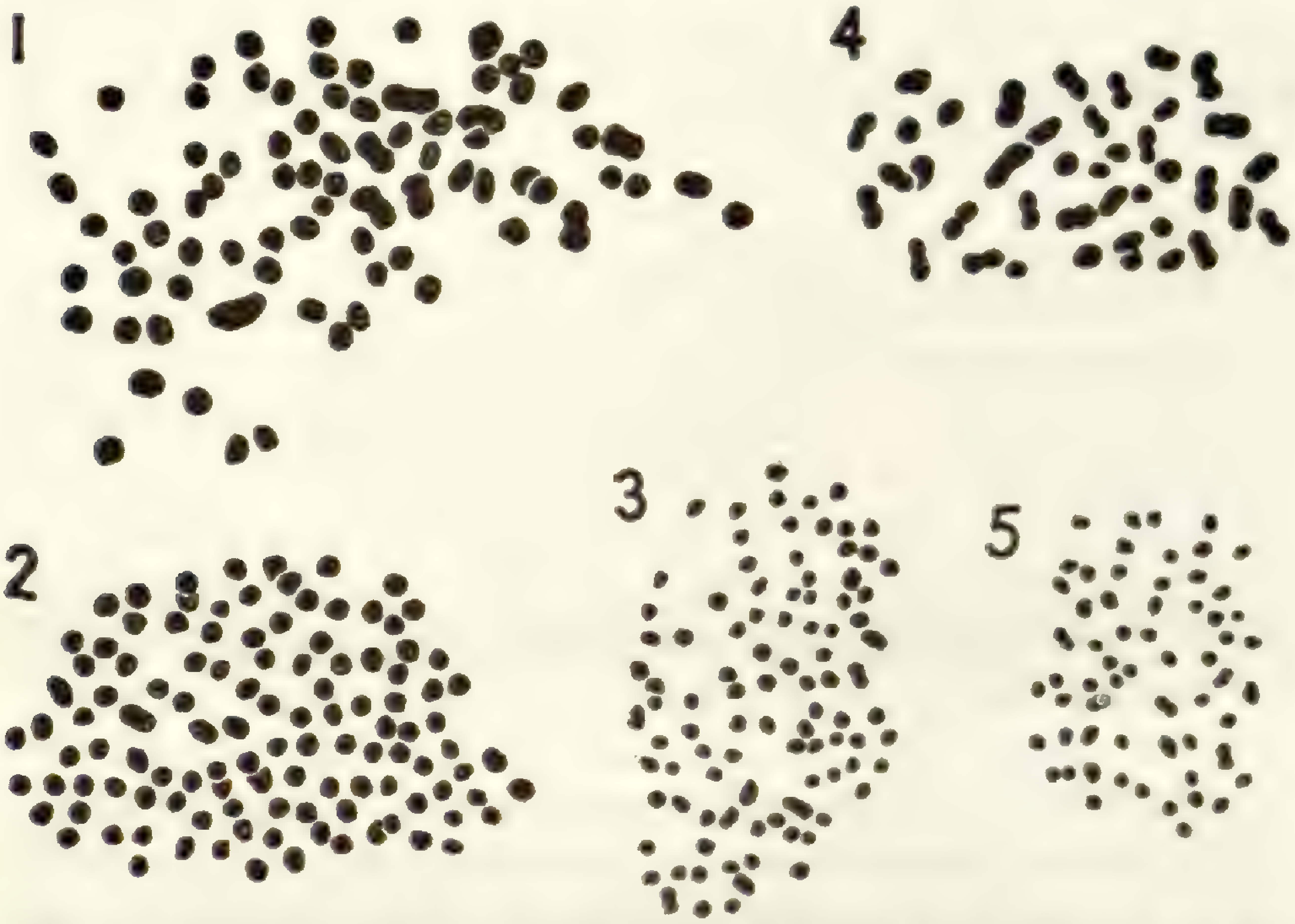


FIG. 19. Root-tip mitoses. 1-4. *Salix glauca*. 1. *Argus 15S*, Churchill, Manitoba (2900X). 2. *Argus 26S*, Churchill, Manitoba (2900X). 3. *Argus 517-58*, Churchill, Manitoba (1960X). 4. *S. brachycarpa* ssp. *brachycarpa*. *Argus 60S*, Churchill, Manitoba (2900X). 5. *S. brachycarpa* ssp. *brachycarpa* × *glauca*, *C. L. Porter*, August 1958, Medicine Bow Mt., Wyoming (1960X).

First, *Salix brachycarpa* ssp. *brachycarpa* is diploid. Second, *S. glauca* from Manitoba may contain more than one level of ploidy. The material counted varies from 4 to 6x, and although the counts are not exact, they are not as high as 10X reported by Löve (1954) for *S. callicarpaea* (= *S. glauca* in eastern Canada). However, it should be noted that the specimens on which these *S. glauca* counts are based represent the ferruginous form of the species (*see* Rocky Mt. phase of *S. glauca*) and due to the uncertainty surrounding this form it cannot be regarded as typical of the eastern Canadian populations of *S. glauca*. Third, the ap-

TABLE III. CHROMOSOME COUNTS OF TAXA IN THE SALIX GLAUCA COMPLEX

Species	Count - ploidy	Source of Material	Reference
Counts reported in the literature, no vouchers seen.			
S. glauca	176 - 8X	Scandinavia ?	Wilkinson (1944)
S. glauca	152 - 8X	Scandinavia ?	Floderus (1931)
S. glauca ssp. stipulifera	152 - 8X	Scandiavia ?	Löve and Löve (1948)
S. glauca (reported as S. callicarpaea)	190 - 10X	Churchill, Man. ?	A. Löve (1954)
Counts reported here, vouchers as indicated			
S. brachycarpa ssp. brachycarpa	40 - 2X	Churchill, Man.	Argus 60S (GWA)
S. glauca	79 - 4X ? 81	Churchill, Man.	Argus 15S (GWA)
S. glauca	95 - 5X	Churchill, Man.	Argus 517-58 (GWA, GH)
S. glauca	102 - 6X ? 115	Churchill, Man.	Argus 26S (GWA)
S. brachycarpa ssp. brachycarpa × glauca	63 - 3X ?	Medicine Bow Mts. Wyo.	Porter Aug. 1958 (GWA)

proximately triploid count obtained for the putative hybrid *S. brachycarpa* ssp. *brachycarpa* × *glauca* lends support to the probability that it is a hybrid, and further suggests that *S. glauca* in the southern Rocky Mts. may be tetraploid.

These data, with the exception of the diploid count for *Salix brachycarpa*, pose more problems than they solve. One important consideration is revealed, namely, that the *Salix glauca* complex in North America is more complex cytologically than had been recognized. As a result, an adequate consideration of polyploidy in this complex must include a sample of material from over the entire range of the taxa involved. Such a survey would be very time consuming and a rapid means for estimating ploidy level would be valuable. The following consideration of a correlation between stomatal length and ploidy level may provide such a tool.

Correlation of Stomata Length and Ploidy Level. The size of stomata, as represented by stomata length, or stomatal frequency has been shown by some workers to be correlated with chromosome number.

In a study of diploid and tetraploid races of *Tradescantia canaliculata*, Karl and Hally Sax (1937) showed a correlation between chromosome-number and cell-size (including number and size of pollen-mother-cells, microspores, stomata, chloroplasts, and stomatal frequency). Using the frequency of stomata per unit area a correlation index was determined. Using this technique they studied several taxa including *Secale cereale*, *Malus*, and *Vaccinium*, where intraspecific polyploidy was found to be widespread.

Stomatal size was used by Randolph (1932) to detect induced tetraploids in *Zea*. In 1938 Greenfield was able to distinguish induced tetraploids and octoploids on the basis of stomata length. In a study of American Hickories, Stone (1961) was able to demonstrate a correlation between ploidy level and stomata size.

In view of these reports of a correlation between stomata size and chromosome-number, an early comment by Camus (1904) that stomata length is constant for certain species of *Salix* takes on a new significance.

In this study the length of abaxial stomata was used as a measure of stomata size rather than stomata frequency (*see* Sax and Sax, 1937) for two reasons. First, error related to the possible variation in the number of stomata per unit area in different parts of the same leaf (Long and Clements, 1934) or between leaves on a single shoot (Sawyer, 1932) could be eliminated; and second, the chance that epidermal cell enlargement may result in more widely spaced stomata could be eliminated.

A comparison of stomata length and chromosome-number in four specimens whose chromosome-number was determined in this study is given in Table IV. A correlation between stomata length and diploidy and polyploidy is

TABLE IV. STOMATAL LENGTH AND CHROMOSOME NUMBER

Species	Chromosome number[1]	Level of ploidy	Stomata length and standard deviation (in microns)
S. brachycarpa ssp. brachycarpa			
Argus 60S, Churchill, Manitoba	40 (38)	2x	18.5 ± 2.5
S. glauca			
Argus 15S, Churchill, Manitoba	79, 81 (76)	4x	27.5 ± 3.5
Argus 517-58 Churchill, Manitoba	95	5x	27.0 ± 2.5
Argus 26S Churchill, Manitoba	102, 115 (114)	6x	26.0 ± 2.5

[1] The actual counts are followed by an estimated chromosome-number in parenthesis based on $n = 19$.

demonstrated, but the several putative levels of polyploidy within *Salix glauca* cannot be detected. Similarly the stomata length data presented in Fig. 2 show a break on a diploid-polyploid line. The diploid taxon *Salix brachycarpa* can be distinguished from the polyploid taxa on the basis of its short stomata. However, the tetraploid *S. arctica* (Holmen, 1952) and *S. arctophila* (Jorgensen, *et al.*, 1958) cannot be distinguished in the same way from the tetraploid to octoploid *S. glauca.*

Within the polyploid *Salix glauca* the eastern Canadian populations can be distinguished from the species in Europe and Asia on the basis of stomata length. This is evidence in support of the lower than octoploid counts obtained for this taxon from Churchill, Manitoba, and conflicts with the decaploid count reported by Löve (1954) for *S. glauca* (as *S. callicarpaea*) from eastern Canada.

An examination of Fig. 2 permits the estimation of ploidy levels in three uncounted taxa. It is probable that *Salix brachycarpa* ssp. *niphoclada* and *S. chlorolepis* are diploids and that *S. brachycarpa* ssp. *niphoclada* var. *fullertonensis* may be represented by two ploidy levels, diploid and polyploid.

It seems clear that although stomata length is potentially valuable in estimating chromosome-number considerably more data, both chromosome-counts and stomata measurements, are required to establish a more definitive correlation. The most that can be said at present is that diploids can be distinguished from polyploids on the basis of stomata length.

Geographic Variation in Stomata Length. If a correlation between stomata length and ploidy level is assumed, a consideration of the geographic variation of stomata length is of taxonomic interest. Consider Fig. 20 in which the mean stomata length is plotted against the geographic distribution of two species, *Salix brachycarpa* and subspecies, and *S. glauca.*

The three infraspecific taxa of *Salix brachycarpa* show a relationship to each other which supports the view that these taxa are more closely related to each other than to *S. glauca* (*see* taxonomy of *S. brachycarpa*). *Salix brachycarpa* ssp. *brachycarpa* is apparently diploid throughout its range. In areas in which it is sympatric (in terms of the geographic units in Fig. 20) with *S. glauca* these taxa can be separated on the basis of stomata length, and presumably chromosome-number. In regions in which convergence is observed in stomata length (i.e. Rocky Mts. (U.S.), Central Alaska, and Arctic Alaska) hybridization is reported to occur and may explain the intermediates (*see* taxonomy of *S. glauca*).

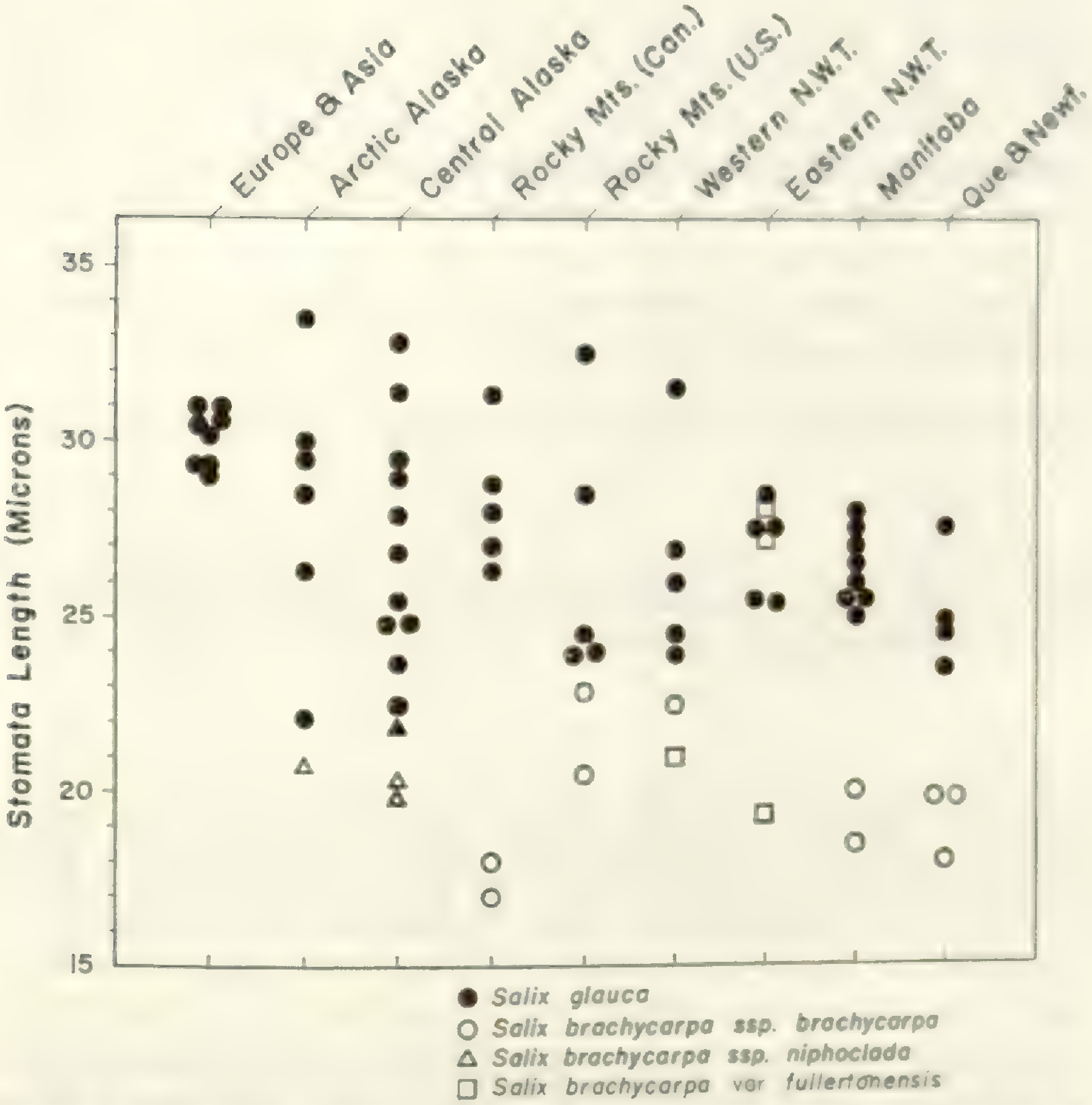


FIG. 20. Geographic variation of mean stomata length in *Salix glauca* and *S. brachycarpa*. Each symbol represents the mean stomata length of one individual (see section Techniques.). See text for discussion.

On the basis of stomata length, *Salix brachycarpa* ssp. *niphoclada* can be assumed to be diploid. Although the sample size is small, this taxon generally seems to differ markedly in mean stomata length, and presumably also in ploidy level from *S. glauca* in Arctic Alaska. The alignment of these taxa, as proposed by Wiggins (Wiggins and Thomas, 1962) is not supported by these data.

There is an indication that *Salix brachycarpa* ssp. *niphoclada* var. *fullertonensis* has a greater tendency toward longer stomata than is typical for the species. In Fig. 20 this variation is shown to be within the limits of variation for the species, and the "tendency" may be due to chance.

The occurrence of intraspecific polyploidy within *Salix glauca,* discussed above, is supported by the data presented in Fig. 20. The mean stomata length, and presumably ploidy level, is greater in Europe, Asia, and northwestern Alaska than in Manitoba and Quebec. In general, there is clinal variation in stomata length from west to east in North America, and there is a possibility of two or three levels of ploidy occurring in this region. Clearly there is a serious need for additional information on chromosome-number in the North American *Salix glauca.*

SOME GEOGRAPHIC ASPECTS OF VARIATION IN SALIX GLAUCA

An examination of a large series of specimens which had been named *Salix glauca, S. cordifolia,* and *S. pseudolapponum* (*glaucops*) revealed the basic similarity of these taxa and suggested that, although populations in certain areas may represent a "typical" manifestation of one or another of these names, there is a large region in which intermediate populations predominate. Furthermore, attempts to distinguish entities to which these names apply break down as soon as the problem is approached on a population basis over a wide geographic area. In order to compare the variation in these taxa the characteristics that have been used to distinguish them were studied over the North American range of the entities concerned. Unfortunately, comparable local populations of *S. pseudolapponum* from the southern Rocky Mountains were not available and the population-variation for this entity is considered only in the northern portion of its range.

In Table V, a comparison is made between *Salix glauca, S. cordifolia* and *S. pseudolapponum* (*glaucops*). The data are derived from the literature (mainly Schneider, 1919 and Raup, 1943 and 1959) and illustrate the difficulty in distinguishing between these presumed taxa. Morphological data based on my observations are recorded in Figs. 21 through 26, and in the systematic treatment; these do not agree in every instance with the data in Table V. Even if the entities

TABLE V

Characteristics	*S. glauca*	*S. cordifola*	*S. pseudolapponum*
Leaf-length	(2-) 4.5-5 (-10) cm.	(1.2-) 3-5 (-6) cm.	not over 4 cm.
Leaf l/w	2.5-4	0.5-2.5	about 2.2
Leaf-shape	Lanceolate, oblanceolate, elliptic-oblong, obovate-oblong or obovate-elliptic.	Elliptic, oval, obovate-elliptic, obovate-oblong or ovate elliptic.	Lanceolate, oblanceolate, elliptic-lanceolate, narrowly elliptic or obovate-lanceolate or elliptic-oblong.
Leaf-apex	Obtuse or acute or nearly short-acuminate.	More or less obtuse or short acute.	Acute to subacute.
Leaf-base	Obtuse or abruptly or gradually cuneate.	Obtuse or broadly cuneate to subcordate.	Cuneate to rounded.
Stipule-length	2.5 to 15 mm.	none to 3-6 mm.	None or much reduced.
Pistillate ament-length	3.5-7 cm. in fruit.	2-5 cm. in fruit.	2-3 cm. in fruit.
Flowering	Loosely flowered toward base.	More or less densely flowered.	Densely flowered.
Capsule-length	7-8 (-9) mm.	6-8 (-10) mm.	6.5-8 mm.
Pedicel-length	¼ to 2 times the glands	Not exceeding glands.	Not exceeding glands.

in Table V are treated in a narrow sense they are difficult to distinguish. However, certain characteristics may be of diagnostic importance and their geographic variation is considered. These are leaf-length, leaf-shape (as length/width), pistillate ament-length, stipule-length, pedicel-length, and petiole-length.

Each of the aforementioned characteristics was studied in twenty-one herbarium samples of local populations. The herbarium samples of local populations were selected from over the North American range of the species, with the exception of the southern Rocky Mountains. The populations were delimited and the characteristics measured in the manner described in the section on techniques. The sample size varies from 44 specimens in the Umiat population (No. 7) to 14 in the Wiseman population (No. 5), with an average of 33 specimens for the 21 populations. The data were plotted as frequency histograms and compared visually. Leaf-length data were plotted on a logarithmic scale to eliminate distortion and more accurately represent comparative intrapopulation variation. If the leaf-length data were plotted on an arithmetic scale the short-leaved eastern populations would appear to have less intrapopulation variation than the long leaved Alaskan populations.

Data from the following local populations are included in Figs. 21 through 26. The geographic area sampled in each population and the sample size are indicated. The populations are:

1. **Naknek,** also including King Salmon, Katmai, Lake Iliamna, Island L., and Ugashik L., 18 specimens. 2. **Mt. McKinley National Park,** 43 specimens. 3. **Fairbanks,** also including Livengood, 25 specimens. 4. **Circle,** also including Miller House and Ft. Yukon, 23 specimens. 5. **Wiseman,** also including Old John L., 14 specimens. 6. **Whitehorse,** also including Lake Atlin, Bennett, Skagway, McRae, and Vista, 26 specimens. 7. **Umiat,** also including Kurupa R., Sadlerochit R., and Saganavirkotk, 44 specimens. 8. **Aklavik,** also including Eskimo Lakes, Eskimo Basin, Williams Isl., Reindeer Sta., Warren Pt., Caribou Hills, and the east branch of the Mackenzie R., 21 specimens. 9. **Jasper National Park,** also including Brule and Beauvert L., 35 specimens. 10. **Glacier National Park,** 16 specimens. 11. **Great Bear Lake,** including Leith Pen., McTavish Arm, Ft. Franklin, Gunbarrel Inlet, Pt. Radium, and Sawmill Bay, 20 specimens. 12. **Great Slave Lake,** including Yellowknife, Barabant Isl., Hardisty Isl., Long Isl., Ft. Rae, Gros Cap Isl., Caribou Isl., Moraine Pt., Indian Village, Ft. Providence, Trout R., and Horn Mts., 28 specimens. 13. **Lake**

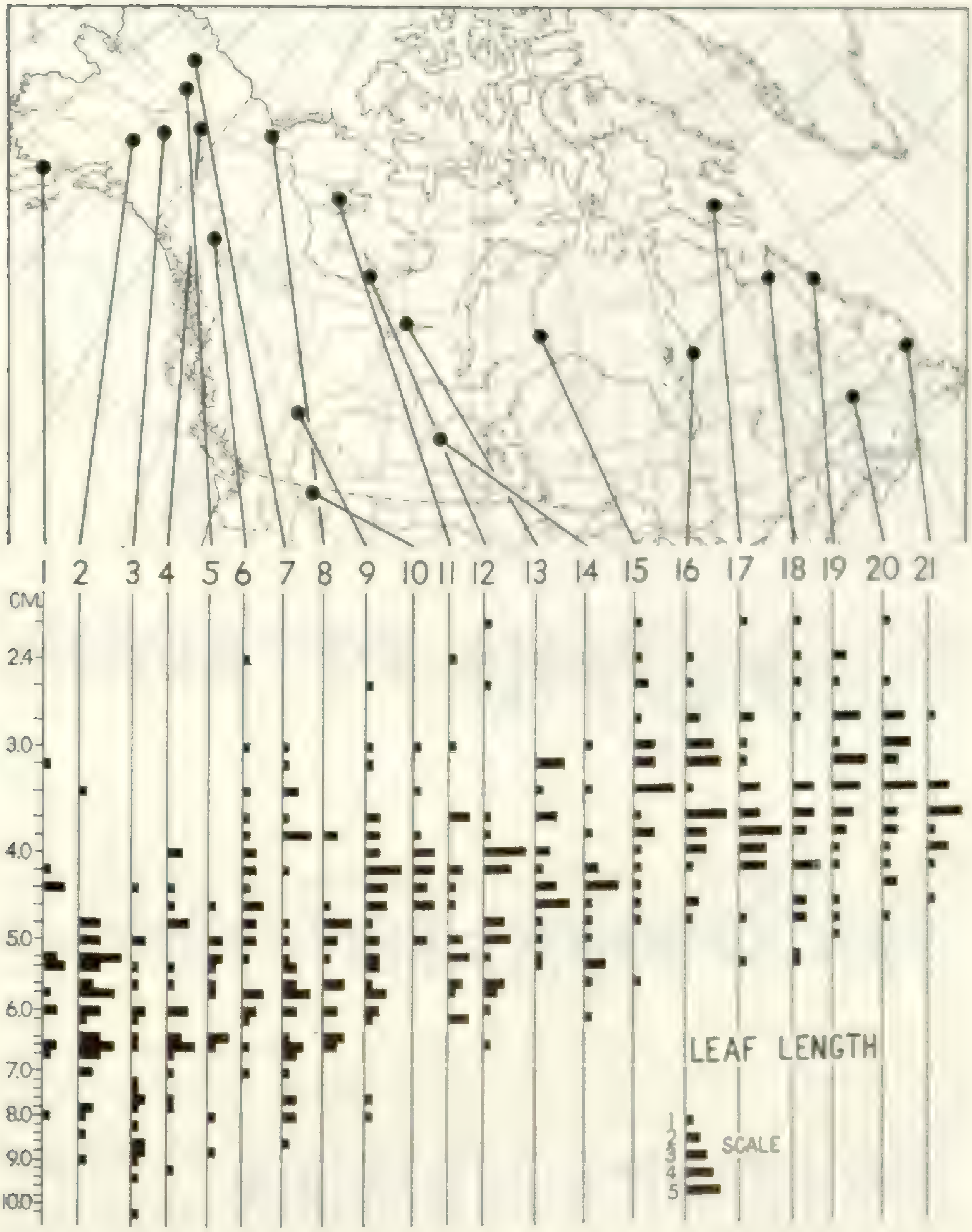
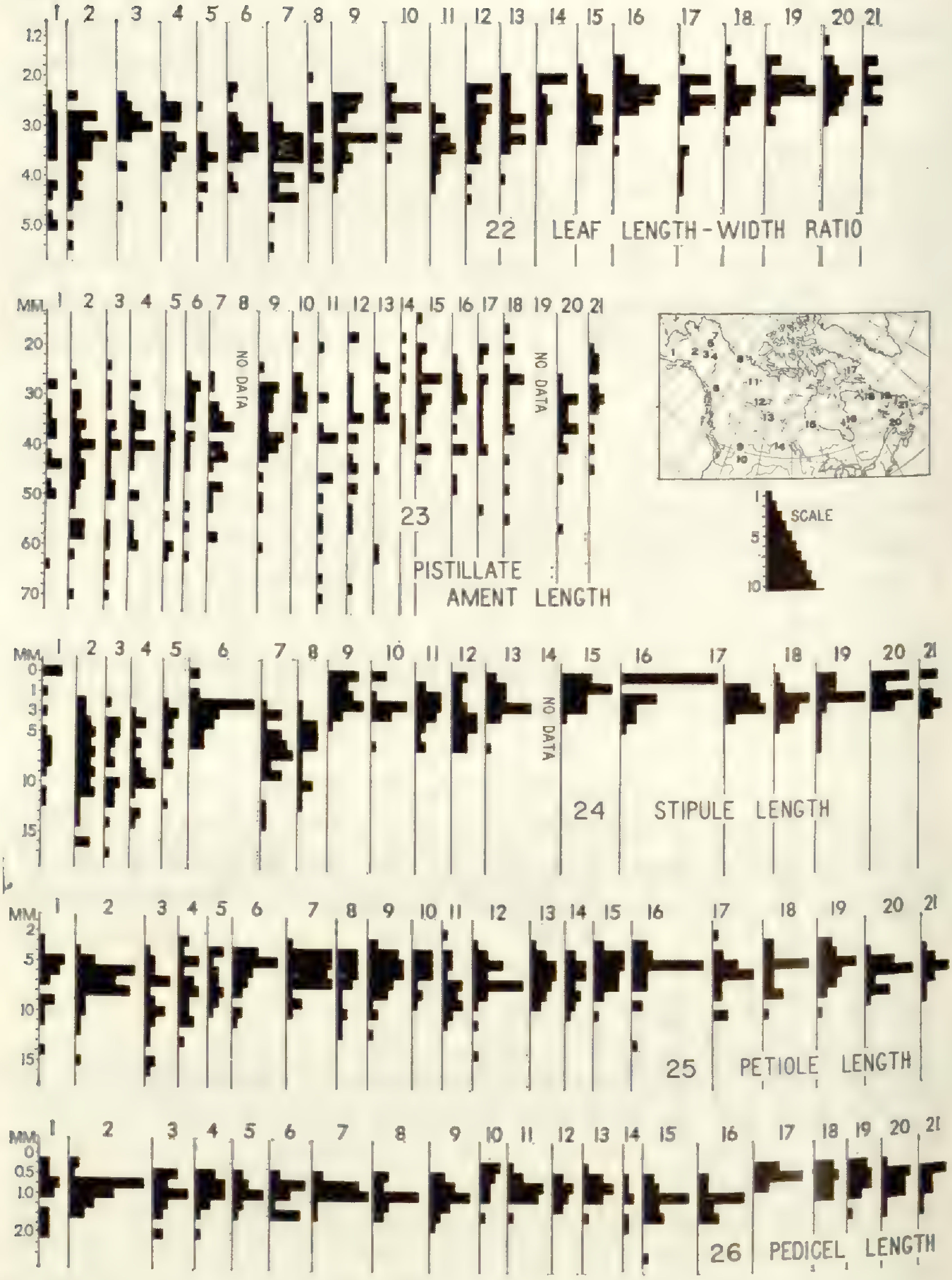


FIG. 21. Geographic variation of leaf-length in *Salix glauca*. See the text for the area represented by each of the 21 herbarium local populations and discussion. The scale is in numbers of individuals. The leaf-length scale is plotted on a logarithmic scale.



FIGS. 22-26. Geographic variation in *Salix glauca*. FIG. 22. Variation in leaf-shape as expressed by the length-width ratio. FIG. 23. Variation in pistillate ament-length. FIG. 24. Variation in stipule length. FIG. 25. Variation in petiole-length. FIG. 26. Variation in pedicel-length. See text for discussion. The scale is in number of individuals.

Athabaska, 23 specimens. 14. **McKague,** also including Tisdale, 18 specimens. 15. **Churchill,** 27 specimens. 16. **Richmond Gulf,** also including Great Whale R., 30 specimens. 17. **Baffin Island,** including Ponds Inlet, Lake Harbour, Pangnirtung, Frobisher Bay, and Griffin Bay, 29 specimens. 18. **George River,** also including Indain House L., Helen Falls, Hades Hills, Mt. Pyramid, Mt. Bridgeman, and Camp Misery, 22 specimens. 19. **Cape Mugford,** also including Windy Tickle, Hopedale, Main, Sumavik, Davis Inlet, Port Manvers, Kikkivitok Isl., Christie Isl., and Jack Lane Bay, 27 specimens. 20. **Mingan Archipelago,** 25 specimens. 21. **Strait of Belle Isle,** including Blanc Sablon, and Forteau, 15 specimens.

Results. Leaf-length (Fig. 21) is strongly clinal from Alaska to eastern Canada. Populations with long leaves occur in the Alaska-Yukon area, and populations with short leaves occur in the Rocky Mountains, eastern, and north-central Canada. The extremes correspond to *Salix glauca* in the northwest, *S. cordifolia* in the east, and *S. pseudolapponum* in the Rocky Mountains. However, connecting the extremes, which more or less overlap, is a series of intermediate populations. Several of the intermediate populations (e.g. Great Slave Lake — 12, Great Bear Lake — 11, and Whitehorse — 6) have a greater intrapopulation variation than do some of the extreme populations (e.g. Fairbanks — 3, Mingan Archipelago — 20, and Glacier National Park — 10). The clinal variation in leaf-length makes this characteristic of much less diagnostic value than had been previously recognized.

Leaf-shape, as represented by length/width (Fig. 22) is also clinal and provides no basis for separating eastern, western, and Rocky Mountain populations.

Pistillate ament-length (Fig. 23) is weakly clinal. Although the eastern and Rocky Mountain populations have slightly shorter aments than the western populations the overlap is too great for this characteristic to be of diagnostic value. The wide intrapopulation variation in ament-length is partly due to the different stages of ontogenetic development represented in the samples. It is difficult to find, in herbaria, sufficiently large collections of individuals in the same stage of development to eliminate this source of error.

Stipule-length (Fig. 24), although slightly clinal, comes closest to providing a characteristic to separate the northwestern populations from the eastern and Rocky Mountain ones. In the Alaska and Mackenzie Delta populations stipules are usually prominent, although sometimes short, and in the eastern and Rocky Mountain populations the stipules are usually short and rarely prominent. However, even in this case the distinction is not unequivocal and there are exceptions which lower its diagnostic reliability such as the Naknek population (No. 1) with many small-stipuled plants and the numerous intermediates in the Mackenzie Delta population (No. 8). The shape of the stipule (not plotted) varies as well as length, with the northwestern populations having narrower stipules than the eastern or Rocky Mountain populations. If the northwestern populations are to be treated as taxonomically distinct from the eastern and Rocky Mountain populations the stipule characteristics may provide some basis for it. In cases in which the stipule is recorded as absent it was either caducous or less than 0.5 mm. long.

Petiole-length (Fig. 25) variation is presented as an absolute value rather than as a ratio for two reasons. One, it illustrates the uniformity of this characteristic throughout North America, independent of leaf-length, and two, if it were considered as a ratio with leaf-length its curve would be similar to that presented for leaf-length. Throughout the entire range of the entities included in *Salix glauca*, petiole-length provides a means to distinguish it from the short-petioled *S. brachycarpa.*

Pedicel-length (Fig. 26) variation has been plotted to illustrate a second characteristic which remains relatively constant over the entire range of the *Salix glauca* complex, and one which is in sharp contrast to the very short pedicel of *S. brachycarpa.*

Discussion. The clinal trends and the wide overlap in characteristics thought to be useful in distinguishing *Salix glauca, S. cordifolia* and *S. pseudolapponum* (*glaucops*) support a treatment of these names as comprising a single species — *Salix glauca.* However, each of these names can be applied to geographic variants of the species which intergrade through a series of intermediate populations. If these extreme variants, the intermediate populations, and Pleistocene events are considered, an hypothesis concerning the evolution of *Salix glauca* in North America can be proposed.

First of all, it is possible to relate the present distribution of each of the variants to a Pleistocene refugium. The Alaska-Yukon variant (*S. glauca* and vars.) may be related to a refugium in central Alaska, western Yukon, and the Arctic Slope of Alaska (Hultén, 1937; Flint, 1957); the eastern Canadian variant (*S. cordifolia* and vars.) may be related to a postulated refugium on the now submerged coastal plain of eastern North America and elsewhere south of the eastern icefront (Hultén, 1937; Raup, 1946); and the Rocky Mountain variant *(S. pseudolapponum)*, not clearly distinguishable from the eastern variant in the data presented here, may be related to complex refugia along the eastern edge of the northern Rocky Mountains (Calder and Savile, 1959) and throughout the southern cordillera which was not continuously glaciated (Flint, 1957). If the populations now represented by these variants survived the Pleistocene glaciations in these refugia they may have evolved their distinctive morphological features here under the combined pressures of different climatic conditions, hybridization, and isolation. However, it is possible that these variants evolved elsewhere and the refugia may represent centers of survival and migration. Just how and when the three variants evolved cannot be determined by the data assembled here. However, if it is assumed that they did evolve from some common ancestry without developing reproductive barriers the numerous intermediate populations now present in the glaciated portion of north central Canada may be attributed to the postglacial migration and "hybridization" of the variants. There is morphological evidence to indicate that since the end of the Wisconsin Stage populations from central Alaska have migrated as far east as Great Slave Lake; that populations from eastern Canada have migrated into the Great Bear Lake region; and that Rocky Mountain populations migrated north to the Yukon and eastward into Saskatchewan and Manitoba. For a discussion of this evidence see the systematic section. The area of overlap of these variants is the area in which the intermediate populations occur (Map 2).

An evolutionary scheme similar to this has been proposed to explain variation in other plant and animal taxa e.g. *Armeria maritima*, Hultén, 1948; *Abies*, Haliday and Brown, 1943; *Rana sylvatica* (wood frog), Martof and

Humphries, 1959; and *Zonotrichia leucophrys* (white-crowned sparrow), Rand, 1948. Although this hypothesis may supply a plausible explanation for the geographic variation observed in the components of *Salix glauca* in North America it may be found to be inadequate after future studies of polyploidy, hybridization, and population-variation. The most important feature of the geographic variation is the intergradation and clinal variation demonstrated for characteristics which have been used to distinguish between the various components of *Salix glauca.*

SYSTEMATIC TREATMENT

KEY TO SPECIES

A. Petiole 3-10(-15)mm. long, usually yellowish; pedicel 0.5-1 (-2) mm. long; anthers usually longer than 0.5 mm.; leaves on reproductive branchlets and proximal leaves on vegetative shoots usually obovate to oblong, apex acute to obtuse; pistillate aments cylindrical, densely flowered. .... *Salix glauca.*

A. Petiole 1-3 mm. long, reddish (except in some ssp. *niphoclada*); pedicel 0-0.25 (-0.5) mm. long; anthers usually shorter than 0.5 mm.; leaves on reproductive branchlets and proximal leaves on vegetative shoots strap-shaped, apex rounded to obtuse; pistillate aments subspherical and densely flowered or narrowly cylindrical and loosely flowered. .... *Salix brachycarpa.*

KEY TO PHASES OF SALIX GLAUCA

A. Leaves generally large, 4-10 cm. long, oblanceolate to narrowly so, L/W 2.8-4; stipules prominent 4-10 (-17) mm. long; pistillate aments 3.5-7 cm. long; bracts light-colored; plants of northwest Canada and Alaska. .... B

B. Leaves often dark-green and glabrescent above, villous-sericeous or sometimes glabrescent beneath; stipules characteristically prominent; pistillate aments stout, long-cylindrical; plants of central Alaska and Yukon, east to Great Slave Lake, N.W.T. .... Western phase.

B. Leaves pubescent on both surfaces, becoming glabrate above, never villous-sericeous beneath; stipules variable in prominence; pistillate aments sometimes slender, not as long as in Western phase; plants of Arctic coastal Alaska and Yukon. .... Beringia phase

A. Leaves smaller than above, 2.4-4 (-5) cm. long, elliptical to obovate, L/W 1.6-3; stipules inconspicuous, 0-4 mm. long; pistillate aments short, 2-4 cm. long; bracts light-colored or sometimes dark; plants of Rocky Mountains, northern Canada east of Mackenzie River, and Greenland. C

C. Shrubs 3-4 (-10) feet tall; branchlets pubescent, becoming glabrescent, often pruinose; leaves narrowly elliptical to oblanceolate; leaves occasionally with ferruginous trichomes; bracts light-brown to blackish; plants of Rocky Mountains, northern British Columbia to New Mexico. .... D

D. Ferruginous trichomes lacking. .... Rocky Mountain phase

D. Ferruginous trichomes on leaves and sometimes on ovaries. .... Ferruginous form of Rocky Mountain phase

C. Shrubs prostrate to 2-3 (-5) feet tall; branchlets white-tomentose to finely pubescent, pruinose in northern Quebec and Baffin Isl.; leaves elliptical to oval or obovate; ferruginous trichomes lacking; bracts light-brown; plants of eastern Canada and Greenland. .... Eastern phase

KEY TO SUBSPECIFIC TAXA OF SALIX BRACHYCARPA

A. Pistillate aments subspherical, if cylindrical then densely flowered; leaves coarsely pubescent on both surfaces; shoot internodes short, leaves appearing fan-like; branches mostly thick and stout; style 0.5-0.8 mm. long; numerous aments borne below vegetative shoots. .... **ssp. *brachycarpa***

A. Pistillate aments long, narrowly cylindrical, loosely flowered; leaves appressed-pubescent beneath, thinly pubescent to glabrescent above; leaf apex acute-attenuate; branches thin and flexible; style 0.2-0.5 mm. long; few aments borne below vegetative shoots. .... B

B. Shrubs usually erect; leaves (2-) 2.5-3.2 (-4.5) cm. long; pistillate aments 2-3.5 (-5) cm. long; bracts narrow, oblong, yellowish; branchlets densely tomentose, yellowish. .... ssp. *niphoclada*

B. Shrubs prostrate; leaves (1.2-) 1.7-2.2 (-2.8) cm. long; pistillate aments 1.5-2.5 cm. long; bracts broad, reddish, drying blackish; branchlets thinly pubescent, reddish brown. .... ssp. *niphoclada* var. *fullertonensis*

Salix glauca L. Sp. Pl. 1019. 1753

Photograph of 1158.52 and 1158.53 in the Linnaean Herbarium, London

Previous treatments have considered *Salix glauca* in North America as three species, an eastern species (*S. cordifolia* and vars.), a northwestern species (*S. glauca* and vars.), and a Rocky Mountain species (*S. pseudolapponum* or *S. glaucops*). On the basis of studies of geographic population variation and the examination of a large series of herbarium specimens I have concluded that these three are conspecific and are best treated as variants of a single wide ranging circumpolar species, *Salix glauca*.

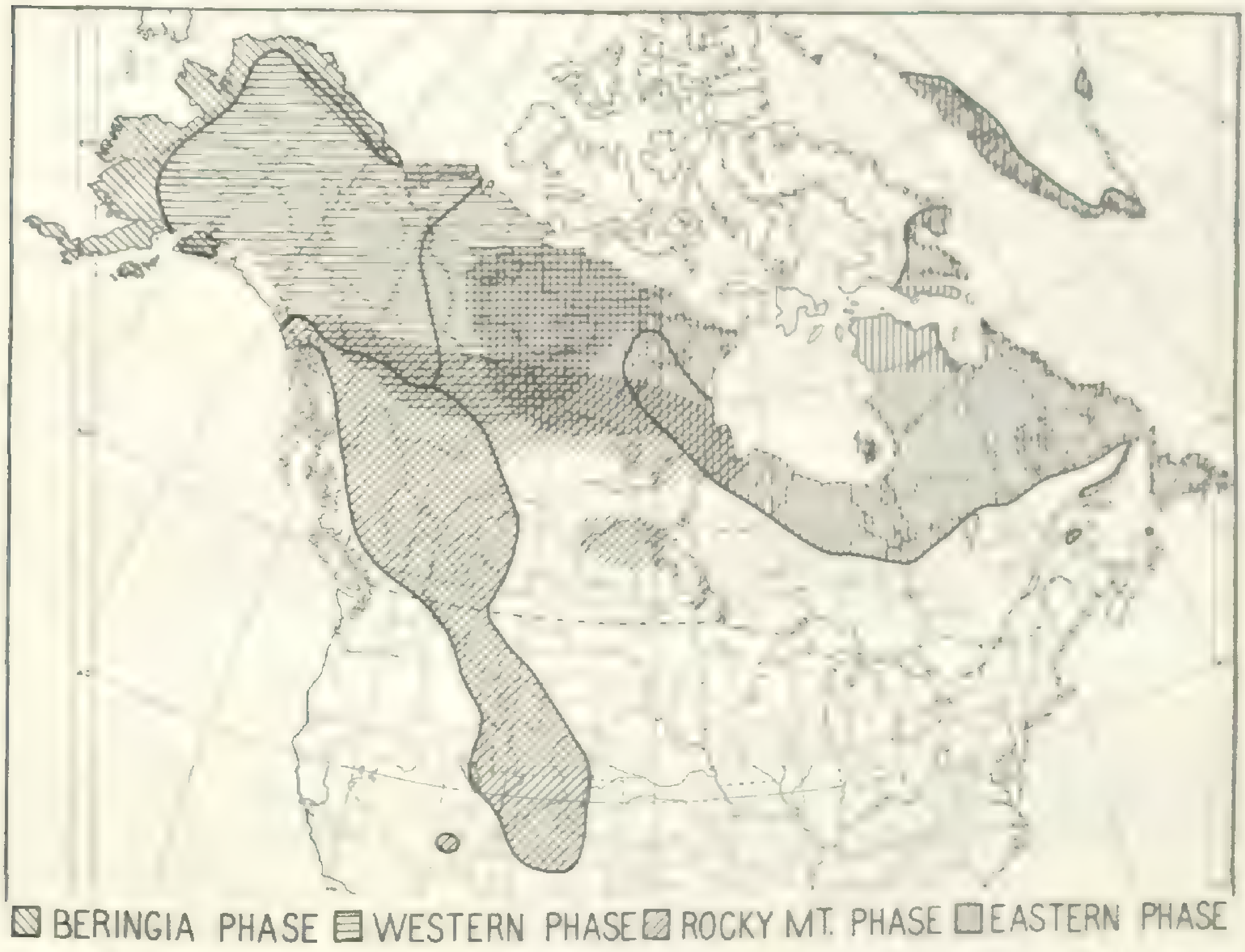
Salix glauca can be distinguished from the related *S. brachycarpa* on the basis of its longer petiole and pedicel, its ovate to oblong leaves borne on the reproductive branchlets and at the proximal end of vegetative shoots, and its stout, cylindrical, usually densely flowered, pistillate aments.

The polyploid nature of the species is reflected in its longer stomata and anthers in comparison to the diploid *S. brachycarpa.*

Only the continental North American range of the species is treated here, although some comments will be made concerning the species in Greenland. It is hoped that the European and Asian representatives of the complex may be studied at a later date when field work is possible.

Map 1. Range map of *Salix glauca* in North America and Greenland.

Within the North American *Salix glauca* a large number of variants have been observed and named by earlier authors. Some of these variants are more or less correlated with certain geographic areas and as geographic variants would commonly be assigned the rank of subspecies or geographic variety. I am reluctant to assign formal nomenclatural rank to these variants for several reasons. First, many of the characteristics used to distinguish the variants vary clinally (*see* section on geographic variation in *S. glauca*) and the area containing intermediate populations is very extensive (*see* Map 2.). Second, the present treatment is concerned only with a portion of the range of *S. glauca,* and until the species is studied in Europe and Asia a well-founded infraspecific classification is impossible. Third, a complete understanding of the variation in this taxon in North America depends on further studies of hybridization, environmental modification, and polyploidy. And fourth, the use of informal nomenclature to designate the major geographic variants seems adequate and will facilitate discussion without implying a final solution or cluttering the already overwhelming nomenclature. For these reasons, the geographic variants of *S. glauca* are termed "phases."



MAP 2. Map of the approximate limits of the phases of *Salix glauca* in North America and Greenland. The areas occupied by the phases, the overlap between them, and the disjunctions are based on herbarium specimens. All boundaries are approxi-

Four phases are recognized in North American *Salix glauca*. Each of the phases has its center in a different geographic area. However, each of the phases is highly variable and their ranges overlap considerably. The *Beringia phase* is centered in arctic coastal and western coastal Alaska, the *Western phase* is centered in central Alaska and the Yukon, the *Rocky Mountain phase* is centered in the Rocky Mountains ranging from British Columbia to New Mexico, and the *Eastern phase* is centered in eastern Canada and Greenland. The major area of overlap between the phases occurs in the western Canadian Shield region (*see* Map 2).

The center of each of the phases may be related to Pleistocene refugia and postglacial migration (*see* section on geographic variation). The variation within each of the phases is complex and hybridization as well as geographic isolation has undoubtedly played a major role in their evolution. In this treatment, a general description of *Salix glauca* in North America will be followed by an amplified description and discussion of each of the phases.

SYNONYMY OF SALIX GLAUCA (Western Hemisphere)

S. cordifolia Pursh, Fl. Am. Sept. **2**:611. 1814. ex char.

S. desertorum Richardson, Frankl. Jour. App. ed. 1:753. (p. 25 in rep.) 1823; ed. 2:765 (p. 37 in rep.). 1823. *Richardson 397*, Ft. Franklin on the Mackenzie River, N.W.T. (K., lectotype; A!, fragment and photograph). *S. glauca* (ssp.?) *desertorum* (Richards.) Anderss. Öfvers. Vet.-akad. Förh. **15**:127. 1858.

S. callicarpaea Trautvetter, Nouv. Mém. Soc. Imp. Nat. Mosc. **2**:295-296. 1832. ex char. and illustration. *S. cordifolia* var. *callicarpaea* (Trautv.) Fernald, Rhodora **28**:184. 1926. *S. cordifolia* ssp. *callicarpaea* (Trautv.) A. Löve, Bot. Not. **1950**:38. 1950. *S. glauca* ssp. *callicarpaea* (Trautv.) Böcher, Meddel. Groenl. **147**:19. 1952.

S. villosa Hooker, Fl. Bor.-Am. **2**:144. 1838. *Drummond 7*, Rocky Mountains, Alberta, Herb. H.B.&T. (K, lectotype; A!, fragment and photograph). *S. glauca* var. *villosa* (Hook.) Anderss. Öfvers. Vet.-akad. Förh. **15**:127. 1858; also Amer. Acad. Arts and Sci. **4**:22. 1858. *S.* × *glaucops α villosa* (Hook.) Anderss. *in* DC. Prodr. **16**:281. 1868.

S. villosa β acutifolia Hooker, Fl. Bor.-Am. **2**:144. 1838. *Richardson 76*, Ft. Franklin on the Mackenzie River, N.W.T., Herb. H.B. & T. (K, lectotype; A!, fragment and photograph; NY!, isolectotype). *S. glauca* var. *acutifolia* (Hook.) Schneider, Bot. Gaz. **66**:327-329. 1918.

S. × *glaucops β glabrescens* Anderss. *in* DC. Prodr. **16**:281. 1868. *Bourgeau*, Rocky Mountains, 1858. (GH!, apparent syntype). *S. glauca* var. *glabrescens* (Anderss.) Schneider, Bot. Gaz. **66**:329-330. 1918. *S. nudescens* Rydberg, Brittonia **1**:86. 1931.

S. desertorum α elata Anderss. *in* DC. Prodr. **16**:281. 1868. *Drummond 660*, Rocky Mountains, Alberta. (GH!, (staminate) syntype?).

S. macounii Rydberg, Bull. N.Y. Bot. Gard. **1**:269-270. 1899. *Macoun 18830*, Ellis Bay, Anticosti Isl., Quebec, 7 Sept. 1883. (CAN, holotype; A!, photograph). *S. rydbergii* Heller, Cat. North Am. Pl. ed. 2:4. 1900. *S. vacciniformis* Rydberg, *in* Britton, Man. Fl. N. St. Can. 319. 1901. *S. cordifolia* var. *macounii* (Rydb.) Schneider, Bot. Gaz. **66**:347. 1918.

S. atra Rydberg, Bull. N.Y. Bot. Gard. **1**:272. 1899. *Bell 18823*, Ford's Harbor, Labrador, 31 July, 1884. (CAN!, lectotype). *S. cordifolia* f. *atra* (Rydb.) Schneider, Bot. Gaz. **66**:346. 1918.

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S. pseudolapponum v. Seemen, Engl. Bot. Jahrb. **29** (65):28. 1900. *Baker, Earle, and Tracy 300½*, Mt. Hesperus, Colorado, 2 July 1898. (NY!, holotype; A!, GH!, MIN!, isotype). *S. wolfii* var. *pseudolapponum* (v. Seem.) Jones, The willow family of the Great Plateau, p. 17. 1908. *S. glauca* var. *pseudolapponum* (v. Seem.) Kelso, Biol. Leafl. **34**:10. 1946.

S. seemannii Rydberg, Bull. N.Y. Bot. Gard. **2**:164-165. 1901. *Williams*, Dawson, Yukon Terr., 12 June 1899. (NY!, syntype). *S. glauca* var. *seemanii* [sic] (Rydb.) Ostenfeld, Skr. Vid.-Akad. Oslo, **1909** (8): 34-35. 1910.

S. cordifolia f. *hypoprionota* Schneider, Bot. Gaz. **66**:346. 1918. *Fernald & Wiegand 3226*, Blanc Sablon, Labrador, 1 Aug. 1910. (GH!, holotype).

S. anamesa Schneider, Bot. Gaz. **66**:348-350. 1918. *Lundholm*, Ilua, Greenland, 15-31 May 1889. (MO!, holotype).

S. glauca var. *acutifolia* f. *poliophylla* Schneider, Bot. Gaz. **67**:61. 1919. *E. & A. Preble 139*, Ft. Rae, N.W.T., 28 July 1901. (US!, holotype). *S. glauca* var. *poliophylla* [as *poliophila*] (Schneid.) Raup. Jour. Arnold Arb. **17**:233. 1936.

S. cordifolia var. *intonsa* Fernald, Rhodora **28**:185. 1926. *Fernald & Long 28030*, Deer Pond Brook, Highlands of St. John, Newfoundland, 20 Aug. 1925. (GH!, holotype & isotype).

S. cordifolia var. *eucycla* Fernald, Rhodora **28**:187. 1926. *Fernald & Wiegand 3204*, Pointe Riche, Newfoundland, 4 Aug. 1910. (GH!, holotype).

S. cordifolia var. *tonsa* Fernald, Rhodora **28**:187. 1926. *Fernald & Long 27971*, Ha-Ha Mt., Newfoundland, 5 Aug. 1925. (GH!, holotype). *S. cordifolia* f. *tonsa* (Fern.) Polunin, Nat. Mus. Canada Bull. **92**:165. 1940.

S. athabascensis Raup, Rhodora **32**:111. 1930. *Raup 8129*, Moose Lake, Alberta, 17 Aug. 1929. (CAN!, holotype; GH!, isotype).

S. fallax Raup, Contr. Arnold Arb. **6**:149-150. 1934. *Raup 4312*, Carbon R., about 4 mi. above Peace, B.C., 2 Aug. 1932. (A!, holotype).

S. glauca var. *aliceae* Ball, Univ. Cal. Publ. Bot. **17**:416-417. 1934. *Eastwood 614*, Whitehorse, Yukon Terr., 12 July 1914. (US!, A!, isotype).

S. pseudolapponum var. *subincurva* Kelso, Rhodora **36**:195. 1934. *Kelso 3503*, Rocky Mt. National Park, 5 Aug. 1931. (GH!, isotype). *S. glauca* var. *subincurva* (Kelso) Kelso, Biol. Leafl. **34**:10. 1946.

S. glauca var. *stenolepis* Polunin, Nat. Mus. Canada Bull. **92**:163-164. 1940. *Malte 118812*, Lake Harbor, Baffin Isl., 25-26 Aug. 1927. (CAN!, holotype).

S. glauca ssp. *desertorum* var. *sericea* Hultén, Fl. Alaska and Yukon **3**:527. 1943. *Mendenhall*, Dall R., 55 mi. above mouth, 23 June 1901. (US!, holotype and isotype).

S. glauca × *farrae walpolei* Cov. & Ball, of Hultén, Fl. Alaska and Yukon, 3:528. 1943. (in part).

S. glauca × *pseudomonticola* Ball, of Hultén, Fl. Alaska and Yukon 3:528-529. 1943. (including the "forms" *subglabra* and *intermedia*).

S. pseudolapponum var. *kenosha* Kelso, Biol. Leafl. 25:3-4. 1944. *L. & E. Kelso* 534, Kenosha Pass, Colorado, 28 July 1936. (personal herbarium of L. Kelso, holotype). *S. glauca* var. *kenosha* (Kelso) Kelso, Biol. Leafl. 34:10. 1946.

S. glauca var. *perstipula* Raup, Sargentia 6:154. 1947. *Raup & Soper 9321*, Brintnell L., N.W.T., 30 June 1939. (GH!, holotype).

DISCUSSION OF SYNONYMY

Salix desertorum Richards. No specific name in this complex has caused more discussion, speculation, and confusion than this one. I have seen a photograph and a fragment of the lectotype *(Richardson 397)* and a sheet considered by Schneider to be identical with the type *(Richardson 70)*. Both of these specimens are juvenile and are similar to other juvenile specimens from Churchill, Manitoba *(Argus 67-58, 68-58,* and *158-58)*, Coppermine, N.W.T. *(Findlay 65)*, and Saskatchewan *(Breitung 75)*. I regard the type-material as representing juvenile material of *S. glauca* as found in central Canada. I agree with Raup (1959) that it has "no viable taxonomic status", but I do not agree that it is necessary to regard it as ". . . an aberrant form of *S. glauca* caused by local site factors . . .".

In 1943, Hultén applied the combination *Salix glauca* ssp. *desertorum* (Richards.) Anderss. to material from western Alaska. He was of the opinion that this combination should be used for the Arctic American *S. glauca* distributed from Newfoundland to Alaska, including material named *S. cordifolia* var. *callicarpaea* by some authors. Again the juvenile condition of the type-material of *desertorum* proved to be a stumbling block and all the material he cited from Alaska (I have seen all but two specimens) was juvenile. Hultén further described a var. *sericea* to include those specimens with leaves densely villous on the lower surface. The type-material of this varietal name is also juvenile and, in this case, it is the common form of the Western phase of *S. glauca*. An understanding of the ontogenetic development of *Salix* would have prevented this unnecessary description of a new taxon. Successive collections from the same shrub made throughout the growing season are useful in acquiring such knowledge. For example, compare *Argus 311* (14 June 1955) and *781* (14 Aug. 1955), both specimens were collected from the same shrub near College, Alaska. The former is similar to var. *sericea* and the latter, using Hulten's classification, to the hybrid *S. glauca* × *pseudomonticola.* Both are simply *S. glauca*, Western phase.

N. J. Andersson, in De Candolle's Prodromus, recognized *S. desertorum* and three varieties, *elata, stricta,* and *fruticulosa.* The latter two are *S. brachycarpa* and will be discussed under that species. The former is a juvenile specimen bearing ferruginous pubescence on the leaves. This form of *S. glauca* will be discussed later in reference to *S. athabascensis* and *S. fallax.*

Salix glauca var. *acutifolia* (Hook.) Schneid. This varietal name has been recognized by many taxonomists with the notable exceptions of N. Polunin and E. Hultén. In 1940, Polunin noted the "fickleness of the characters" which identify it, and preferred not to recognize this or any other variety of *S. glauca.* Hultén (1943) referred much of the material called var. *acutifolia* to his hybrid *S. glauca* × *pseudomonticola.* It is supposedly characterized by leaves mostly acute at the apex and somewhat smaller and more narrowly elliptic or lanceolate than the typical form. Raup (1959) is of the opinion that var. *acutifolia* shows geographic segregation which justifies its varietal status. The holotype *(S. villosa β acutifolia* Hook., *Richardson 76),* of which I have seen a fragment and a sheet of the isotype, does have leaves that are sharply acute at the apex and narrower than usual; but this material is young, and other, better developed, Richardson collections *(72* and *73)* have leaves noticeably broader and less acute or with nearly obtuse apices. I cannot agree that this name represents a taxon that is of any value to the interpretation of the species. Its characteristics are highly variable and are influenced both by the age of the plant and by the environment.

Salix glauca var. *stenolepis* Polunin. This name was given to material from northeastern and central Canada, ". . . intermediate between *S. glauca* and *S. cordifolia,* although approaching much more closely the former." It was characterized by long narrow bracts and stipules. The holotype has persistent narrow stipules about 4 mm. long, and in the paratypes the stipules may be narrow as in *Soper 132196* or very small as in *Malte 126895*. The bracts of the pistillate aments averaged about 2.5 mm. long and I could not find any 3-4 mm. long as described. I feel certain that the characteristics used to distinguish this variety are insignificant in the species. It is remarkable that Polunin, noted for his refusal to recognize any of the other varieties of *Salix glauca*, should have described it at all.

Salix glauca var. *perstipula* Raup. This name was described in 1947; however, Raup later equated it with var. *stenolepis* after he saw Polunin's type and noted that its stipules also were persistent. The var. *perstipula* was characterized by ". . . conspicuous, lance-attenuate, persistent stipules." Although some American *S. glauca* do have persistent narrow stipules I do not feel that this characteristic deserves any greater stress than any other single characteristic. Furthermore, it has not been shown that it has any significant geographical or genetical importance, and it may simply represent an ecological modification.

Salix glauca var. *acutifolia* f. *poliophylla* Schneider and *S. glauca* var. *aliceae* Ball have been used to identify material with permanently pubescent leaves and shoots. The former (f. *poliophylla*) was based on material from Great Slave Lake, N.W.T. Only one specimen was considered typical and others were thought to be intermediate between it and var. *acutifolia*. When Raup (1936) found that several of his collections from Lake Athabasca *(Raup 4508* and *4597)* had a similarly dense leaf pubescence he felt that this characteristic had a ". . . geographic affinity in the central part of the Mackenzie basin . . .", and therefore deserved varietal status. He later (1947 and 1959) equated it with var. *aliceae*.

When Ball described var. *aliceae* he knew of Schneider's form but it is difficult to tell if he regarded it as synonymous with his variety or not. He claimed that var. *aliceae*, which "inclines toward *S. cordifolia*", differs from *S. glauca* in its broader leaves sometimes with subcordate bases, broader stipules, longer capsules 8-10 mm.), and in the usually undivided styles. From the isotype before me (*Eastwood 614*, Whitehorse, Yukon Terr.) I cannot understand Ball's characterization. The leaves and stipules are certainly no broader than the species, the bases of the leaves are rounded, not subcordate, and long capsules are more typical of the species than his variety. Ball's concept of this name changed with time and whereas in the beginning he included those specimens which were permanently pilose, he later included many specimens with leaves sericeous-tomentose below and glabrescent above, typical of the species in central Alaska. Our knowledge of pubescence-variation does not support the use of this characteristic as a proper basis for recognizing infraspecific taxa.

Salix glauca × *pseudomonticola*, f. *subglauca* and f. *intermedia* of Hultén. In his treatment of *Salix* for the Flora of Alaska and Yukon, Hultén (1943) was very much influenced by the possibility of hybridization in the genus. The bulk of the material formerly called *S. glauca* var. *acutifolia*, var. *glabrescens*, and var. *aliceae* was identified as hybrids. I fully agree with comments by Ball and Raup that evidence of hybridization, especially between these two species, is difficult to support. Although hybridization does occur in *Salix* there is no concrete evidence for the origin or presence of this hybrid and to base an unwieldy taxonomy on such an untested hypothesis is undesirable (*see* discussion of hybrids).

Salix glauca × *farrae walpolei* of Hultén. Six specimens from the Bering Straits District of Alaska were cited under this hybrid name (Hultén, 1943). One of the specimens *(Jones 9045)* was also cited as the only representative in Alaska of *S. fullertonensis*. After examining all but one of the cited specimens I find that two species are included in the material, *S. glauca* (*Kellogg, 29 Aug. 1909; Jones 9034;* and *Anderson 5002*), and *S. brachycarpa* ssp. *niphoclada* (*Jones 9045;* and *Walpole 1752*).

Salix athabascensis Raup and *S. fallax* Raup. It is with some hesitation that I include these names in *Salix glauca*. Both may represent hybrids including *S. glauca* × *pedicellaris* or even *S. pedicellaris* × *planifolia*. The origin of these forms is highly uncertain and they are treated here as synonymous with *S. glauca* because of numerous intermediates linking them to *S. glauca* in populations at Churchill, Manitoba, northeastern Saskatchewan, and in the northern Rocky Mountains. The material which represents these two names is very interesting and its relationship to *S. glauca* deserves careful study. *Salix athabascensis* was described in 1930 and based on material from northeastern Alberta. The type-material is in late fruiting condition. Its glabrous capsules, long pedicels, and coriaceous leaves suggested *S. pedicellaris* Pursh, and its putative relationship to that species was discussed. *Salix fallax* was described four years later from material from eastern British Columbia. This material is also in late fruiting condition. It was tentatively related to *S. pedicellaris* but no mention was made of *S. athabascensis.* In neither of this discussions of these species was *S. glauca* mentioned, although that species is strongly suggested by several characteristics, including the pubescent ovaries, pedicels, stems, and leaves; the narrow neck of the ovary and capsule, and the long style. Material from the Canadian Rocky Mountains shows all forms of intermediacy between *S. athabascensis, S. fallax,* and *S. glauca.*

The first taxonomist to note the resemblance of *Salix athabascensis* and *S. fallax* was Breitung (1957) and Scoggan (1957) apparently concurred in this judgment. A. J. Breitung made numerous collections throughout central Saskatchewan which have contributed importantly to the understanding, such as it is, of these names. A characteristic of these "species" which has not been noted previously is the occurrence of ferruginous trichomes on the leaves. These rusty-colored trichomes are often rare but sometimes very common and may render the structure reddish in color. This characteristic has been subsequently found throughout central Canada from Hudson Bay westward and definitely seems to link these names to the glabrescent forms of *S. glauca.* The type material of *S. desertorum α elata* Andersson also bears ferruginous trichomes and further relates *S. athabascensis* and *S. fallax* to *S. glauca.*

Salix pseudolapponum v. Seem. This names has been applied to *Salix glauca* in the southern Rocky Mountains. I am unable to distinguish this small leaved alpine form from

S. glauca and prefer to regard it as a portion of the Rocky Mountain phase of that species.

The Eastern phase of *Salix glauca* is represented by what has been called *S. cordifolia*, with numerous varieties and forms. The basic outline of its infraspecific classification was presented by Fernald in 1926. The variation in the Eastern phase is similar to that described in the Western phase, and I do not propose to recognize any of the variants as more than forms or ecological modifications.

Salix cordifolia Pursh. I have not seen the type-specimen of this name, but the description gives a clear picture of it, and specimens having similarly broad leaves with cordate bases are known from Newfoundland *(Fernald & Long 27078, 27977; Fernald & Wiegand 3219)*. The material in the Hooker Herb. from G. Anderson's garden, of which I have seen a tracing, does not have the broad cordate leaves of Pursh's description, but rather looks like *S. callicarpaea*.

Salix callicarpaea Trautv. and *S. cordifolia* var. *callicarpaea* (Trautv.) Fernald. These names represent the most common form of *S. glauca* in eastern Canada. I have not seen the type of *S. callicarpaea* and my judgment is based on the description and figure, both of which adequately characterize it. I agree with Schneider (1918b) that Trautvetter's concept of *S. cordifolia* and *S. callicarpaea* merely represents two stages of the same species. The former name is based on fruiting material and the latter name on flowering material. The name *callicarpaea* is characterized by its more or less glabrate leaves which are oblanceolate to elliptic with acute bases. Although this form is abundant throughout eastern Canada, it intergrades with the Western phase west of Hudson Bay.

Salix glauca ssp. *callicarpaea* (Trautv.) Böcher. In his discussion of *S. glauca* in west Greenland Böcher includes the "smooth Greenland willows" in this combination. He does not agree with other taxonomists that the Greenland willows should be called *Salix callicarpaea* because it and *S. glauca* are not distinct enough to be regarded as two species. In this area he recognizes two "ecologically and morphologically different types", one broad-leaved and hairy on sunny exposures, presumably *S. glauca*, and the other narrow-leaved and smooth and growing in moister places, *S. glauca* ssp. *callicarpaea.* If the Eastern phase of *Salix glauca* is to be treated as a subspecific entity this is the name that should be used.

Salix cordifolia var. *macounii* (Rydberg) Schneider. I have not seen the type of *S. macounii,* but the description and the specimens later referred to the variety by Fernald depict a low, spreading shrub with small leaves tending to be elliptical to obovate with acute apices. This form intergrades in one direction with var. *eucycla* Fern., whose leaves are more or less orbicular and rounded at the apex, and in the other direction with var. *callicarpaea.* Even one specimen can almost span this variation *(see Fernald, Long, & Dunbar 26570).* It may be that the material from Newfoundland with its orbicular leaves may represent introgression with *S. arctica.* Many of our specimens show other characteristics of *S. arctica* as well, including pruinose buds and stems, long straight trichomes on the underside of the leaves producing a "beard" at the apex.

Salix cordifolia var. *tonsa* Fernald and var. *intonsa* Fernald. These names describe extremes of pubescence-variation. The first is the glabrous form and the latter the pubescent form. Numerous intermediates connect the two making their value as varieties doubtful. Polunin (1940) reduced var. *tonsa* to a form on the grounds that it lacked any geographical range. In commenting on this reduction Raup (1943) wrote, "To be consistent, one should perhaps reduce them all (*i.e.* the other varieties of *S. cordifolia*) to forms, since some of the others show scarcely any better geographic segregation than does var. *tonsa.*"

Salix anamesa Schneider. After examining the type of this name I find it to be simply *S. glauca.* I cannot find any sign of *S. arctica* in it, although hybridization between *S. glauca* and *S. arctica* is apparently common in Greenland. The *Salix* of Greenland are in need of a careful field study before the complexities found there can be understood.

GENERAL DESCRIPTION OF SALIX GLAUCA

Erect shrubs 1 to 3 feet tall, sometimes up to 15 feet, or prostrate. Branches reddish-brown to grayish, the epidermis often flaky, glabrate or variously pubescent, often with persistent pubescence, sometimes pruinose. Branchlets pubescent to white-tomentose, sometimes pruinose. Buds reddish-brown, pubescent and pruinose similar to the branchlets.

Leaves highly variable in shape and size, from oval or suborbicular to narrowly lanceolate; length/width (1.2-) 2.0-3.8 (-5.4); length 3-9 cm. in the west, 2.5-4.5 cm. in the east. Apex acute to attenuate, obtuse or sometimes rounded. Base tapering, acute or sometimes obtuse or cordate. Margin generally entire, sometimes with glands along the lower third of blade which may be raised on small teeth. Blade green above and glaucous beneath, often glossy above. Blade-pubescence varying from villous-tomentose on both sides to more commonly glabrate above and pubescent below. Petiole always longer than the bud, (2-) 4-10 (-16) mm., pubescent or glabrate and mostly yellowish. Stipules present, minute to 0.5-8 (-17) mm. long, glandular-margined, generally glabrous, variously persistent.

Staminate aments coëtaneous, cylindrical, borne on reproductive shoots generally shorter than those of the pistillate aments. Bracts light-brown to stramineous, ovate to oblong, pubescent on both sides to glabrate on the outer surface, usually with short wavy trichomes, sometimes with long straight trichomes. Glands usually in pairs, one adaxial and the other abaxial. The adaxial gland usually larger and often cleft into two lobes. The abaxial gland usually narrow, short and uncleft. Filaments two, free or united at the base, glabrous or pubescent near the base. Anthers reddish in preanthesis, light brown in postanthesis.

Pistillate aments coëtaneous, cylindrical, borne on short leafy reproductive shoots (peduncle of authors). Ament-length (1.4-) 2.2-5.0 (-7) cm. long. Bracts as in the staminate flowers. Ovaries white-tomentose or pubescent. Capsules sparsely pubescent to almost glabrate, long-beaked and light-brown. Pedicel (0.25-) 0.5-1.5 (-2.5) mm. long, pubescent. Gland adaxial, commonly simple and flattened, sometimes two-lobed, usually shorter than pedicel. Style one, 0.5-1 mm. long, entire or variously divided into two lobes. Stigmas two, each two-lobed, often as long as the style.

BERINGIA PHASE. FIGS. 29 & 30

Principal Synonymy. *Salix glauca* and *S. glauca* ssp. *desertorum.*

Amplified Description. Shrubs prostrate to more commonly erect, 1 to 3 feet tall, individuals in favorable locations up to 9 feet tall. Branchlets white-tomentose, some simply pubescent. Leaves generally oblanceolate, some narrowly so, apex and base acute to attenuate. Blade usually pubescent on both sides, becoming glabrate above in age, the pubescence beneath sometimes of short appressed trichomes, never of the villous-sericeous type. Blade-size and -shape similar to the Western phase (Figs. 21 & 22), with a tendency to be shorter. Petiole often very short. Stipules varying from very short to over 10 mm. long, occasionally absent. Pistillate aments generally shorter than in the Western phase and loosely flowered, approaching the narrowly cylindrical type found in *S. brachycarpa* ssp. *niphoclada.* **Styles predominately divided, rarely entire.**

FIGS. 27-30. *Salix glauca.* FIGS. 27 & 28. Representative European specimen. *V. Samuelsson 569*, 18 June 1920, Lappland, Sweden. FIG. 27. General view. FIG. 28. Closeup of pistillate ament. FIGS. 29 & 30. Representative of the Beringia phase. *A. Johnson, et al. 610*, 5 Aug. 1959, Bering Straits District, Alaska. FIG. 29. General view. FIG. 30. Closeup of pistillate ament. *A. Johnson, et al. 303*, 5 July 1959, Bering Straits District, Alaska.

Distribution (Map 2). The Beringia phase occurs from westernmost Alaska Peninsula, probably including Unimak Island, eastward to Kodiak Island and Lake Iliamna. Northward along the coast of western Alaska to the Seward Peninsula thence eastward across the Arctic slope of Alaska into the Mackenzie River delta area, N.W.T. The morphological similarity of the species throughout this crescent is the reason for its inclusion in one phase and it is not a suggestion that the phase represents a single Pleistocene isolate.

There is some doubt whether *Salix glauca* occurs on the Aleutian Islands, although it is known from the nearby Shumagin Islands and the Alaska Peninsula. I have seen a specimen (*Beale*, 11 June 1941) from Unimak Island which may be in the *Salix glauca* complex; however, its juvenile condition and insect damage preclude positive identification. The westernmost specimen of positive identity is *Schofield 2331* from Cold Bay, near the tip of the Alaska Peninsula.

Discussion. The Beringia phase is, in some parts of its range, virtually inseparable from "typical" European *Salix glauca* (compare Figs. 27 & 28 with 29 & 30). The material I have seen from Kodiak and the Shumigan Islands is remarkable in this resemblance and undoubtedly Coville's (1901) opinion concerning *S. glauca* was strongly influenced by his experience with the species in this area. However, there is also a tendency for it to approach *S. brachycarpa* ssp. *niphoclada* in certain characteristics. This is especially noted in juvenile specimens. Characteristics such as narrow leaves, short petioles, and narrowly cylindrical aments, which ordinarily identify ssp. *niphoclada* are also found in the Beringia phase and they must be appraised with caution. *Salix brachycarpa* ssp. *niphoclada* occurs over most of the range of the Beringia phase with the exception of Kodiak Island and the western Alaska Peninsula. In these latter areas *S. glauca* does not seem to vary in the direction of ssp. *niphoclada*, suggesting that the intergradation elsewhere is the result of hybridization and introgression. The effect the environment may have in the formation of apparent intergrades is unknown. This problem is an important one on the Arctic slope and the Seward Peninsula. The populations on the Arctic slope could, for example, be regarded as hybrid swarms and the "typical" species infrequent. A case for this view could be supported by the herbarium material I have seen. However, in the absence of experimental information concerning the relative influence of hybridization and the environment, it seems to be an undesirable one. In my treatment I have used *S. glauca* in a somewhat broader sense than *S. brachycarpa* ssp. *niphoclada.* Hybrids have been recognized only when they are fairly certain. Actually, *S. glauca,* as characterized here, probably includes many specimens of hybrid origin. Herbarium material, in spite of its abundance, is still inadequate for a clear understanding of this problem.

Intergradation of the Beringia phase and the Western phase occurs in the Cook Inlet and the foothills of the Arctic Slope regions. The former area is possibly a region where migrants from the Alaska Range and the Alaska Peninsula overlap, and the latter where migrants from central Alaska entered the Brooks Range.

Ecology. The habitat of the Beringia phase varies widely. On the Arctic Slope, Spetzman (1959) reports it from floodplains and cutbanks especially on the sand shores of rivers and streams. On the Alaska Peninsula it also occupies tundra habitats, and on Kodiak Island it occurs on sea cliffs, *Carex, Sphagnum* swamps, and grassy slopes.

SELECTED SPECIMENS. **Alaska:** Western Pacific Coast district: Shumagin Is., Sand Pt., *Coville & Kearney 1800* (US); *Griggs,* 31 July 1913 (US); Cold Bay (opposite Kodiak Is.), *Beals 57* (NA); Naknek L., *Cahalane 20*, 24** (US), Katmai, *57** (US); Fox Bay, *Griggs,* 28 July 1913 (US); Naknek, *LePage 24054** (DAO), *24056** (NA); Belkofsky, *O. Murie 2070B** (NA); Naknek airfield, *K. Raup 42** (US), 58°45′, 156°37′, *75** (MIN, US), Island L., *207** (US), Upper Ugashik L., *239** (US), King Salmon Cr., *326** (US); King Salmon, *Schofield 2057A** (DAO, GH), *2193** (DAO, GH, NY, RM), *2259** (DAO, NY), *2599*, 2604*, 2650** (DAO), Cold Bay, end of Alaska Pen., *2331* (DAO); Kodiak Is.: Sturgeon R., *Coville & Kearney 2248* (US); Raspberry Is., *Eyerdam 3776;* Olga Bay, *E. & H. Looff 914* (A, NA, NY); Kodiak, *Walpole 1155* (US). Central Pacific Coast district: Lake Iliamna, *Gorman 90** (NA, NY, US), *139** (US). Bering Sea district: Port Clarence, *Coville & Kearney 1875* (A, US); Golovin, *Enander,* 9 Sept. 1928 (A); Ogotoruk Cr. drainage, *Johnson, Viereck, & Melchior 41, 168, 170, 303, 610, 643, 644, 645,* (ALA, GWA); Nome, *Jones 9034* (DS, NA); *Enander,* 11 Sept. 1928 (A); *Anderson 5002* (NA); *Kellogg,* 29 Aug. 1909 (US); Teller, *Scamman 5453,* Kotzebue, *3995* (GH); Kotzebue Sd. and Norton Sd., *B. Seemann 1423,* Chamisso

Is., *1793* (NY); Noatak and Kugururuk R., *Spetzman 4209* (MIN, NA); Imuruk Basin, Cobblestone R., *Walpole 1687* (US). Arctic Coast district: Cape Lisburne, *Anderson 4498* (NA); Pitmagea R., *Cantlon & Gillis 57-254*, Jago L., *57-110* (GH); Okpilak L., *Cantlon & Malcom 59-237* (GH); 69°26′, 151°28′, *Chambers 165** (DS); Umiat, *Churchill 134*, 166b*, 192*, 216*, 221a*, 283*, 373*, 383*, 385*, 386*, 494*, 496*, 548*, 563a*, 618*, 763**, (NA); *LePage 23594** (NA); *Wiggins 12931** (DS, RM); *Hodgdon 8939**(US), *8973*, 8974** (GH), Kurupa R., *8890** (US); Kurupa L., *Hodgdon & Riedeman 8602** (GH), above jct. of Kurupa and Coville Rs., *8904** (DAO); Pitmegea R., *Shetler & Stone 3298* (GH, MICH); Kanayut Cr., *Spetzman 1991* (DAO, MIN, NA), Sadlerochit R., *1033** (MIN, NA), Canning R. and Ignek Cr., *3884* (MIN); East Oumalik, *Ward 1502** (DS, RM). **Yukon:** Firth R., *McEwen 164* (CAN); Head Pt., *Oldenburg 44352* (GH); between King and Kay Pts., *A. Porsild 7131* (CAN); King Pt., *Lindstrom*, 4 July 1906.

WESTERN PHASE. FIGS. 31-33

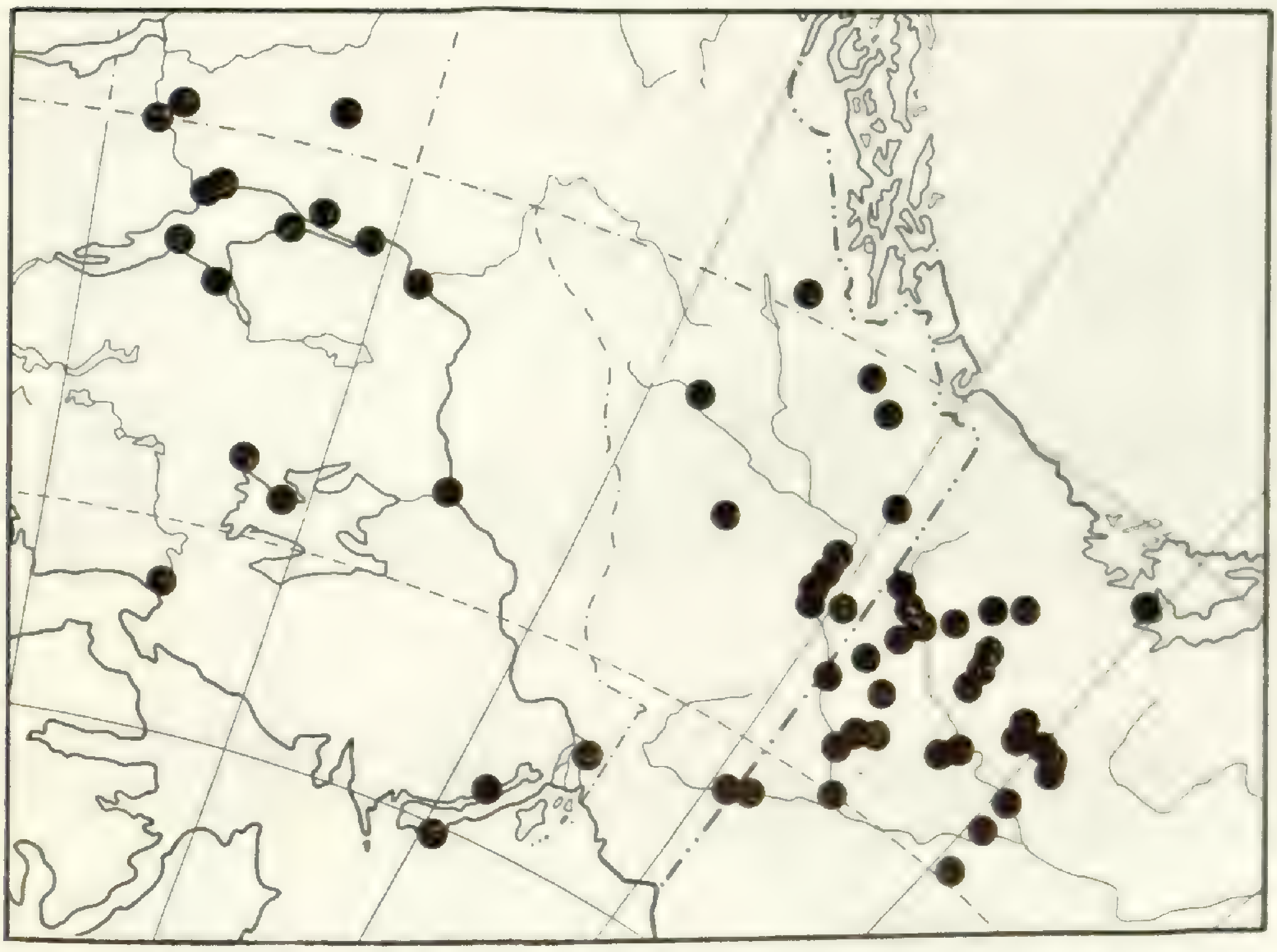
Principal Synonymy. *Salix glauca* var. *acutifolia*, *S. glauca* var. *glabrescens*, *S. glauca* var. *aliceae*, *S. glauca* var. *stenolepis*, *S. glauca* ssp. *desertorum* var. *sericea*, and *S. glauca* × *pseudomonticola (padophylla)*.

Amplified Description. Erect shrubs 3-7 or up to 15 feet tall. Branchlets long and pubescent, not tomentose, but sometimes densely pubescent, especially in the northern and eastern parts of the range. Leaves generally oblanceolate, 4-10 cm. long, characteristically dark-green and glabrescent above, and white villous-sericeous (in 50% of the specimens) or sparsely appressed-sericeous to glabrescent beneath. Petiole long, but shorter in relation to leaf-length than the Eastern phase. Stipules long and prominent, rarely absent. Pistillate aments long and densely flowered, but often loosely flowered at the base. Styles predominantly divided, but entire styles occur in 30-40% of the specimens.

Distribution (Map 2). The Western phase of *Salix glauca* occurs throughout the western and central parts of Alaska and eastward to the Yukon Territory and into the Great Bear Lake and Great Slave Lake region. In Alaska it extends northward into the Brooks Range where it overlaps the Beringia phase and southward into the Cook Inlet and Coastal Mountain area where it also overlaps the Beringia phase. In the vicinity of Great Slave Lake there is a major transitional region where the Western, Eastern, and Rocky Mountain phases overlap and intergrade extensively. The southern edge of the Yukon Plateau, near the British Columbia border, seems to represent the southern limit of this phase and here a narrow transitional region between it and the Rocky Mountain phase can be detected.

Figs. 31-33. Representative specimens of the Western phase of *Salix glauca*. Figs. 31 & 32. *G. Argus 613*, 21 July 1956, Alaska Range, Alaska. Fig. 31. General view, note prominent stipules and variation in the attenuation of the leaf apex. Fig. 32. Closeup of pistillate ament. Fig. 33. Close-up of staminate ament. *G. Argus 1008*, 9 June 1957, College, Alaska.

Discussion. The Western phase of *Salix glauca* is best developed in the central Alaska-Yukon Plateau region. Its most striking characteristic is its villous-sericeous leaf-pubescence which is often correlated with a robust aspect, including large leaves and stipules. Although there is considerable variation within the phase, specimens of this phase can be readily segregated out of a series of collections. The central Alaska — Yukon Plateau region may have served as a refugium for *Salix glauca* during the Pleistocene glaciations and it is possible that sometime during this isolation the Western phase evolved its unique character. The characteristic of villous-sericeous leaf-pubescence is distinct enough so that it can be plotted on a map (*see* Map 3) and used as an indication of extent of migration. The phase probably had its center in central Alaska and from there spread in all directions. Although the map does not show its occurrence in western Alaska this is probably due to insufficient collecting in the area. To the eastward it reaches its apparent limit near Fitzgerald on the Slave River, and to the north it can be traced along the Porcupine River into the Mackenzie River Delta region and thence eastward to Coppermine, where it is relatively abundant. In the Alaska Range it is prominent and as far south as the Coast Ranges it retains its identity, although it becomes highly variable in habit, leaf-size and pubescence, and ament-length. The wide variation in this part of Alaska may be related to 1) the wide range of habitat variation in this mountainous region,



MAP 3. The distribution of villous-sericeous leaf-pubescence in the Western phase of *Salix glauca*. This characteristic is very abundant in central Alaska and western Yukon and becomes less common to the eastward.

2) hybridization with *S. brachycarpa* ssp. *niphoclada,* or 3) to intergradation with the Beringia phase.

Two major transitional areas between the Western phase and other phases deserve discussion. The first is the transition between the Western phase and the Rocky Mountain phase located in the general area of the Yukon — British Columbia border along the southern edge of the Yukon Plateau. The herbarium local population at Whitehorse, Y. T. (population No. 6, Figs. 21-26), although within the boundaries of the Western phase, shows a definite tendency toward the Rocky Mountain phase in its shorter leaves, stipules and aments, a lower leaf-length/petiole-length ratio, as well as a general absence of villous-sericeous leaf-pubescence. Even as far north as Dawson, Y. T. certain influences possibly attributable to the Rocky Mountain phase can be detected. In this area there is an increase in glabrescence in leaves, shoots and aments. Such glabrescent individuals have been described by Schneider as var. *glabrescens* and by Hultén as *S. glauca* × *pseudomonticola* f. *subpseudomonticola.* The leaves are glabrescent or finely sericeous beneath and bear glands on the margin. These glands are not unique, but are simply more noticeable on the glabrescent specimens. The ovaries are sericeous, becoming glabrate in age. In some respects these specimens suggest the ferruginous form of the Rocky Mountain phase (*see* below) except for the absence of rusty colored leaf pubescence.

The second major transition occurs between the Western phase and the Eastern phase in the region between Great Bear Lake and Great Slave Lake. The species in this region is well illustrated by the herbarium local population study (Figs. 21-26). The populations from Great Bear Lake and Great Slave Lake are intermediate in most of the characteristics studied and smooth out an otherwise stepped cline (*see* section on geographic variation in *S. glauca*). The many specimens I have studied from the Great Slave Lake area support the view that intergradation between the phases is almost complete in this region. Individuals characteristic of the Western phase (Fig. 34) (*Thieret & Reich 4963, 4637, 7748; Thieret 4316; Lewis 849*), and those characteristic of the Rocky Mt. and Eastern phases (Fig. 35)

FIGS. 34-35. Representatives of *Salix glauca* from the transitional region between the Western, Eastern, and Rocky Mountain phases. FIG. 34. A specimen of the Western phase type from Great Slave Lake: note the oblanceolate leaves and the long aments which relate it to the Western phase and the very small stipules which suggest the Eastern or Rocky Mt. phases. *Thieret & Reich 7748*, 15 July 1951, N.W.T. FIG. 35. A specimen resembling the Rocky Mt. or Eastern phases from the Horn Mt., west of Great Slave Lake. This specimen bears scattered ferruginous trichomes on its leaves. *Thieret & Reich 5927*, 30 July — 2 Aug. 1959, N. W. T.

(Thieret & Reich 4728, 5027, 5859, 5927, 5923; Lewis 842) are represented, but the majority of the specimens are intermediate. The influence of the Eastern phase becomes more evident in the northern Lake Athabasca region. As discussed below, the Rocky Mountain phase also probably plays a role in modifying the variation of *Salix glauca* in central Canada, but the differences between it and the Eastern phase are so subtle that the influence of the two cannot be separated.

Ecology. The Western phase of *Salix glauca* is principally a shrub of forests and muskegs. In central Alaska and the Yukon it is very common in *Picea mariana* muskegs and occurs in openings and along drainage channels in *Picea glauca* forests. In the mountainous parts of Alaska, Yukon, and the Northwest Territories it also occurs in the forests, but here it extends into the subalpine *Salix, Betula* scrub, slide rocks, and in some areas above timberline. It is one of the pioneers on glacial outwash plains and is frequent along the gravel floodplains of glacier-fed rivers. In the western Northwest Territories it is prominent in the scrubby tundra as well as in muskegs and forests.

SELECTED SPECIMENS. **Alaska:** Central Yukon district: Harding L., *Scamman 6486** (GH); Salcha Slough, *O. Murie*, 19 June 1922* (NY, US); Fairbanks, *Palmer 154** (NA); College, *Argus 287** (GWA, RM), *311* (GWA, RM), *436*, 781* (DAO, GWA, RM), *1008, 1009*, 1020*, 1106*, 1163*, 1164*, 1165*, 1166*, 1167*, 1168*, 1169*, 1171*, 1174** (GWA), Chena Bluffs, *363** (GWA, RM); Ester Dome Rd., *Williams 819** (NA); Alatna R., 30 mi. above mouth, 1901 (US); Galena, *Péwé F-125* (NA); Ruby, *Rouse 46* (NA); Kaltag, *W. & C. Setchell 459a*, Nulato, *495* (NA); Pedro Dome, *Argus 569** (GWA, RM), Livengood Rd., 38 mi. from jct. with Steese Hwy., *1193** (GWA); Livengood, *Scamman 1717*, 4888** (GH); Steese Hwy., Mi. 140, *Cody & Webster 5352** (DAO); Miller House, *Scamman 121*, 733*, 2042*, 5165** (GH), Independence Cr., *3493B** (GH); Circle, *Anderson 2505** (NA); *Dutilly, LePage, & O'Neill 20920** (NA); *W. C. Setchell 389** (MIN, NA), *390*, 542** (NA), *543** (GH, NA, US), *544** (NA); *Williams 489** (NA); Circle Hot Springs, *Scamman 125** (GH); Ft. Yukon, *Georgeson 13** (US); *Henderson 15036*, 15041*, 15044** (NA); *Scamman 128** (GH); *W. & C. Setchell 403*, 405** (NA); Old Rampart, *Buckley 153* (GWA); Wiseman, *Anderson & Gasser 5816*, 5819** (NA); *Lutz 817** (NA, NY); *Scamman 132** (GH), *899** (GH, US), *2237** (GH, GWA), *2237B** (GWA); Middle Fork of Koyukuk R., *Marshall*, 18 Aug. 1929* (NA); Arctic Village, *Jordal 3626**, mountains NW of Old John L., *3788**, Old John L., *3825** (NA); *Shetler 948*, 1146** (ALA, GWA); *Smith 2554b**

(GWA). Central Pacific Coast district: Kenai Pen., Ptarmigan L., *Klein 60* (NA); between Skilak and Tustumena L., *Palmer 5, 51, 58* (NA); Anchorage, *LePage 23461* (DAO, NA); *O. Murie*, 2 Aug. 1922 (US); Tazlina Gl., *L. & T. Viereck 2192* (GWA); Chitina, *W. & C. Setchell 52* (GH, NA); Kennicott Gl., *L. & T. Viereck 2207* (GWA). Alaska Range district: Mt. McKinley Nat. Pk.: Teklanika R., *Argus 612** (GWA, RM), *613** (DAO, GWA, RM), *615**, *617** (GWA, RM), Camp Eielson, *642*, Camp Denali *649** (GWA, RM), *650** (GWA), *651** (DAO, GWA, RM), Toklat R., *683** (GWA, RM), Igloo Cr., *691** (DAO, GWA, RM); Mi. 6, *H. & V. Bailey 4612**, *4613**, Mt. Healy *4652**, between Toklat R. and Polychrome Pass, *4853**, Savage R., *5012**, *5030** (NA); Toklat Camp, *Bolinger 18** (NA); Savage R. camp, *Henderson 15054a** (NA); Muldrow Gl., *Mexia 2137** (A, MIN, NA, NY), *2138** (A, GH, MIN), Wonder L., *2245**, *2264** (A); Mile 1, *A. Murie 2**, Mile 7, *56**, Mile 50, *117**, *124**, Mile 69, *19**, Igloo Cr., *16**, *28** (NA), *66a** (NA, NY); Park Headquarters, *A. & R. Nelson 3627** (NA, RM, US), Mi. 35, *3688** (GH, NA, RM, US), *3691** (NA, RM, US), Igloo Cr., *3764** (GH, NA, RM, US), Polychrome Pass, *3779** (NA, RM, US), Toklat Cabin, *4094** (GH, NA, NY, RM, US); Savage R., *W. & C. Setchell 192** (GH, NA); Thorofare R., and Glacier Cr., *Viereck 1095** (GH, GWA), Wonder L., *Viereck 1713** (DS, MIN), Mi. 70-80, *1775** (GH). Phelan Cr., *Argus 1145* (GWA); Richardson Hwy., Mi. 242, *Cody & Webster 5730* (DAO); Summit L., *W. & C. Setchell 104b* (NA); Black Rapids Gl., *L. & T. Viereck 2133* (GWA). **Yukon:** Bear Cr., *Calder & Billard 3221* (DAO, MIN, US); Dawson, *Eastwood 386, 504* (A, NA, US), *812* (A); *Williams*, 12 June 1899 (NY); Hunker Cr., *Macoun 54385* (GH, NY); Mayo, *Gillett & Mitchell 4205* (DAO); Whitehorse, *Anderson 9606** (NA); *Gillett 3838**, *3845** (DAO); *Gillett & Mitchell 3246**, *4421**, *4514** (DAO), *3247** (DAO, RM); *Porsild & Breitung 9142** (GH, US); Teslin, *Argus 274* (GWA); Canol Rd., Mi. 105, *Porsild & Breitung 9244* (GH, US); Mi. 127, *10012*, Mi. 132, *9511*, Mi. 136-138, *9777* (GH, NY, US); Burwash, *H. Raup, Drury, & K. Raup 13975* (A); Kluane L., *H. & L. Raup 12217, 12430* (A). **Northwest Territories:** District of Mackenzie: Mackenzie Mts., Brintnell L., *H. Raup & Soper 9228, 9321, 9409, 9421, 9509, 9630, 9632* (A, ALA, CAN, RM, UBC); Mackenzie R. delta, east channel, *Cody 10353**, Eskimo L. Basin, *10103A** (DAO); New Aklavik, *Cody & Ferguson 9846**, Reindeer Sta., *10024**, *10026**, *10032**, *10033**, Williams Is., *10391**, Eskimo L., *10455**, *10474**, *10525**, *10598**, *10675**, *10782**, *10828** (DAO); Aklavik, *Cody & Gutteridge 7896**, *7913** (DAO); Caribou Hills, *Cowan 54** (DAO), *A. Porsild 16879** (GH); Aklavik, *Dutilly 18060** (GH, NA).

ROCKY MOUNTAIN PHASE. FIGS. 36-39

Principal Synonymy. *Salix* × *glaucops*, *S. pseudolapponum*, *S. glauca* var. *pseudolapponum*, and in the northern Rocky Mountains and Plains *S. fallax* and *S. athabascensis*, in part.

Amplified Description. Shrubs generally 3-4 feet tall, but ranging from 10 inches to 13 feet. Branchlets pubescent, commonly becoming

FIGS. 36-39. Representative specimens of the Rocky Mountain phase of *Salix glauca* in Colorado. FIG. 36. General view of a pistillate specimen in fruit. *Smith 1779*, 11 Aug. 1946, Trail Ridge, ca. 11,500 feet, Colorado. FIG. 37. Closeup of pistillate ament in flower. *Levi 3*, 23 July 1959, near Gothic, Colorado. FIGS. 38 & 39. Staminate specimen of *S. glauca*. *Smith 832*., no date, Trail Ridge, ca. 11,500 feet, Colorado. Fig. 38. General view. Fig. 39. Closeup of staminate ament, note the dark-colored bracts.

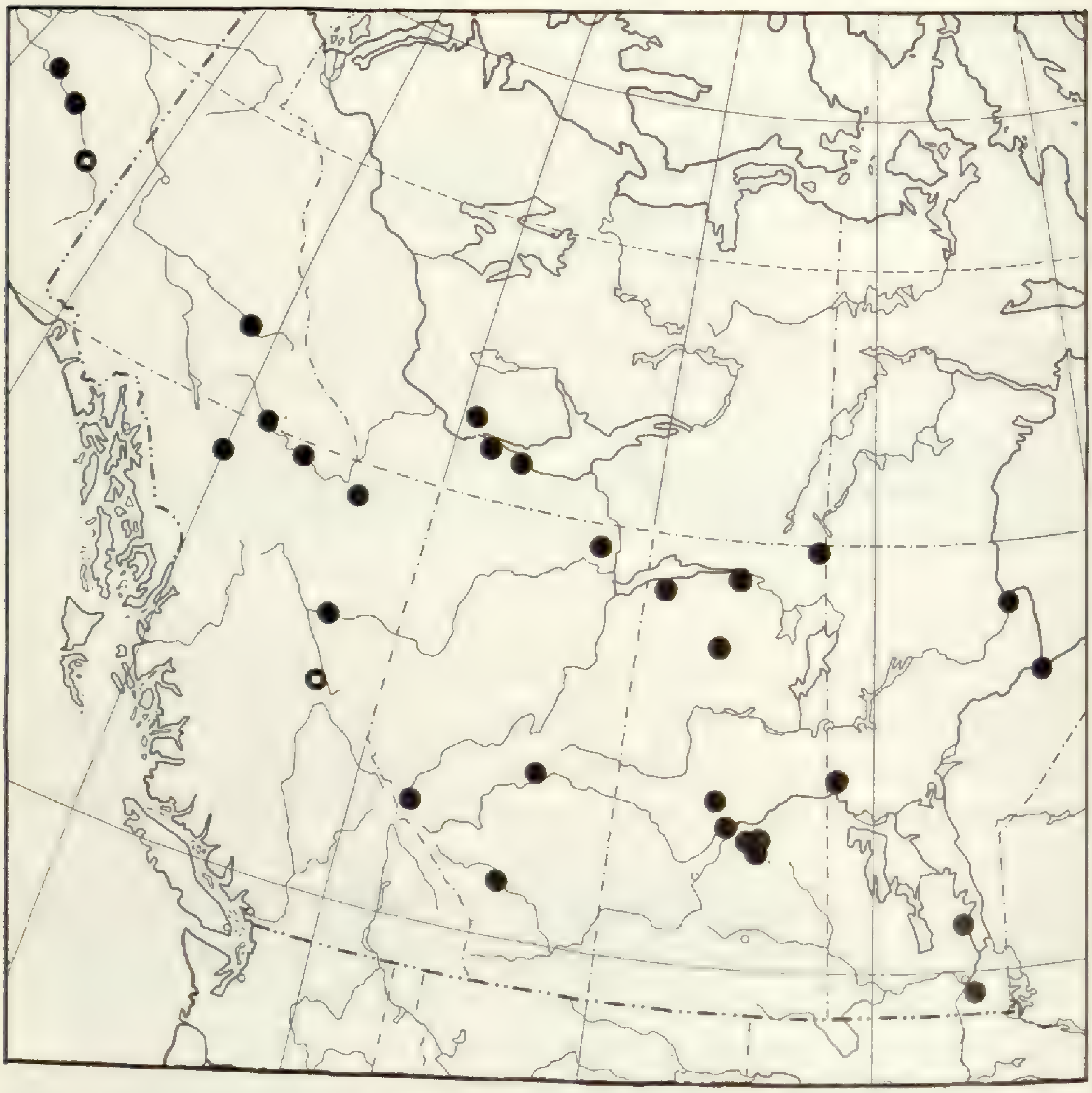
glabrescent, often pruinose. Leaves generally small and narrowly elliptical, sometimes oblanceolate, pubescent on both sides or glabrescent. Stipules present, mostly less than 0.5 mm. long, up to 4 mm. long in some. Pistillate aments usually short and densely flowered, sometimes long and loosely flowered. Ovaries tomentose, capsules tending toward glabrescence. Pedicels ranging from 0.25-1-1.75 mm. long. Styles short, about 0.5-0.8 mm. long, predominantly entire.

Distribution. The Rocky Mountain phase of *Salix glauca* occurs in the mountains of British Columbia, Alberta, Montana, Wyoming, Colorado, New Mexico, and Utah. Its apparent influence extends northward into southern Yukon and the Northwest Territories, and eastward across Saskatchewan and into Manitoba, as far east as Churchill and York Factory. It is primarily a mountain element which overlaps the Eastern phase in the boreal forest and subarctic region between the Rocky Mountains and Hudson Bay.

Discussion. The Rocky Mountain phase differs from the other phases in degree only, and individual specimens are often difficult to assign to this phase unless their geographic location is known. This phase is generally characterized by a tendency toward glabrescence in leaves, stems, and capsules, its short leaves, short undivided styles, and short to absent stipules. These characteristics are all in marked contrast to the Western phase and it is possible to distinguish between the two even in the zone of intergradation in southeastern Yukon. However, the contrast with the Eastern phase is less well marked and presumably the intergraduation between these phases is more complete than between the Rocky Mt. phase and the Western phase.

For purposes of discussion the Rocky Mt. phase will be divided into two parts, the northern Rocky Mountain phase and the southern Rocky Mountain phase. The dividing line between these parts can be represented by the International Boundary between the United States and Canada.

An interesting feature of the variation in the northern Rocky Mountain phase is the occurrence of ferruginous trichomes. This, so-called, ferruginous form occurs widely throughout central Canada from eastern Manitoba to western Alberta, and northward (Map 4). It is of special interest because in some areas it comprises a significant portion of the populations and two names, *Salix fallax* and *S. athabascensis*, have been based on it.



Map 4. The distribution of ferruginous leaf- and capsule-pubescence in *Salix glauca*. This type of rusty-colored pubescence is relatively common in Saskatchewan and Manitoba and is frequent in Alberta. The open circles represent specimens which are similar to the ferruginous form but lack the characteristic rusty-colored trichomes.

In addition to the occurrence of ferruginous trichomes this form has sparsely pubescent to glabrescent leaves, stems, and capsules, long pedicels (about 1.5-2 mm. long), and widely spreading capsule-valves. Although sometimes this form can be segregated on the basis of the above characteristics they are more often randomly distributed throughout *Salix glauca* in the northern Rocky Mountains eastward to Hudson Bay. In the region north of Lake Athabasca and in parts of the Canadian Rocky Mountains, thinly pubescent to glabrescent individuals lacking ferruginous trichomes are common (*see* the open circles on Map 4). In northeastern

Saskatchewan and Churchill, Manitoba complete intergradation has been observed between glabrescent and pubescent leaves and stems, glabrescent and pubescent ovaries and capsules, long and short pedicels, and ferruginous and colorless trichomes; so that any attempt to distinguish two taxa on the basis of these criteria becomes hopeless.

The ferruginous form raises the question of the importance of hybridization to the variation-pattern of *Salix glauca*. The limited distribution of the ferruginous form in central Canada and its frequent association with sterile, putative hybrids, suggest that hybridization may be instrumental to its formation. This possibility is supported by the resemblance of this form to other species and by the frequent occurrence of sterile ovaries. Its leaves often resemble those of *S. pedicellaris* in shape, texture, and venation *(Raup 9122, 10998, 1101; Thieret & Reich 4630;* and *Jack 2749)*. The long pedicels resemble those of *S. pedicellaris* in *Breitung 106, 166*, and *542*. The ferruginous pubescence may be linked to *S. planifolia, S. scouleriana*, or perhaps *S. maccalliana*. The occurrence of patchy pubescence on the ovaries also has been noted in the hybrid *S. brachycarpa* × *chlorolepis*.

In some areas these indications of hybridization are more common than in others. Along the southern edge of the boreal forest in Saskatchewan (McKague) and as far north as the Lake Athabasca region the ferruginous form of *Salix glauca* may occur in company with *S. pedicellaris, S. planifolia* and apparent hybrids of these taxa. In this region we may have the hybridization of three taxa producing a complex hybrid swarm, or it is possible that some specimens referred to the ferruginous form of *S. glauca* are really the hybrid *S. pedicellaris* × *planifolia*. However, in other areas including Churchill, Manitoba, indications of hybridization are absent and the ferruginous form occurs in populations in all habitats. Specimens such as *Argus 517-58, 490-58, 456-58; Breitung 2154;* and *Scoggan 6062* and *6088A* represent the ferruginous form and yet produce good seed and show no obvious signs of hybridization.

In this treatment the ferruginous form is dealt with as a part of the Rocky Mountain phase of *Salix glauca*. At the same time, I recognize that some of the individuals which exhibit this character are probably hybrids which in some cases may not even include *S. glauca.* Any attempts to recognize this variant as a specific taxon (either *S. fallax* or *athabascensis*) seem unsupportable at this time. Studies now underway in northern Saskatchewan may result in a clarification of this problem and perhaps a modification of this treatment.

The southern part of the Rocky Mountain phase, particularly in southern Wyoming and Colorado, presents such a high degree of complexity that I have been unable to fully understand it on the basis of herbarium material alone. The phase in this area has long been a source of confusion (Ball, 1899; Schneider, 1918b; and Smith, 1942) and will require detailed field study to be fully resolved. As has been noted previously, in this area *Salix glauca* has gone under the name *S. pseudolapponum* or *S. glaucops.* The literature reveals perennial confusion and vacillation concerning the nature and diversity of the species in this area. Rydberg (1917) recognized *S. pseudolapponum, S. glaucops, S. seemannii,* and *S. desertorum*; the latter two names are synonyms of the Western phase of *S. glauca.* Smith (1954) recognized *S. pseudolapponum, S. glauca glabrescens,* and *S. cordifolia,* the latter names representing the Western and Eastern phases respectively. Kelso described several varieties of *S. pseudolapponum* which he later (1946) transferred to *S. glauca* as his concept of the species changed (*see* discussion of synonymy). Each of these authors recognized that *S. glauca* occurs in the southern Rocky Mountains in some form but they generally hesitated to refer all of their material to that species. An examination of a large series of specimens makes the reason for the confusion evident. For, although the material has certain distinctive characteristics such as plane, glabrate, short-petiolate leaves; glabrescent capsules; dark bracts; yellow branchlets; and stomata in the upper epidermis, there are present all degrees of intermediacy between these populations and *S. glauca* of the Western and Eastern phases. All efforts to distinguish the southern Rocky Mountain populations from *S. glauca* have failed and it seems most accurate to regard them as a part of the Rocky Mountain phase of *S. glauca.*

Three factors which seem to have influenced the variation of *Salix glauca* in the southern part of the Rocky Mountains are hybridization, isolation, and phenotypical modification. Hybridization has probably played a major role. I suspect that hybridization has been, and is, more widespread in this part of the species range than in any other part of North America. *Salix brachycarpa* ssp. *brachycarpa* seems to be commonly involved in hybridization with *S. glauca* and in some areas, such as the Medicine Bow Mountains of Wyoming, hybrid swarms may occur. Hybridization has gone on to such an extent that neither of these species is completely recognizable (Argus, 1957). However, an accurate assessment of the situation will require field-study and experimentation. Other species which may be involved in hybridization with *S. glauca* are *S. arctica*, *S. wolfii*, *S. wolfii* var. *idahoensis*, and *S. eastwoodiae* (including *S. orestera*).

The second factor, isolation, raises the question of recent morphological divergence of populations. Repeated reference has been made to the influence of the Pleistocene glaciations and the importance of isolation to the divergence of the major phases of *Salix glauca*. However, today in the southern Rocky Mountains there exists a reverse situation in which populations which were probably more continuous during the Wisconsin glaciation are now relatively isolated in what may be called "interglacial refugia". Populations in such areas as the Big Horn Mts., and the Medicine Bow Mts. of Wyoming, in southwestern Utah, and throughout the mountains of Colorado, are probably more isolated than the range-maps would suggest. The degree to which such isolation permits genetical divergence is as yet unknown for *S. glauca* and its relatives, but it may prove to be considerable.

The third factor, phenotypical modification, should be evaluated, especially in reference to elevation. Specimens from Colorado (H. Levi) and Wyoming (C. L. Porter) which were cultivated in the greenhouse and nursery at Boston, Massachusetts, showed such a remarkable phenotypical plasticity that the importance of such modification must be given careful consideration. Phenotypical modification may assume greater importance than usual in the southern Rocky Mountains where great environmental extremes are so closely related to elevation differences. This problem will require field study coordinated with transplant experiments.

Ecology. The Rocky Mountain phase occurs in a variety of habitats from openings in spruce woods, groves of _Populus tremuloides_, pine forests, and along river and lake shores below timberline. It is less abundant on alpine slopes in the Canadian Rocky Mountains, although in the Rocky Mountains of the United States it is very abundant in both alpine and subalpine situations, and occurs up to 12,000 feet in parts of Colorado. The ferruginous form seems to be most common in _Picea mariana_ muskegs and bogs along the southern edge of the boreal forest extending northward; it also may occur in willow thickets along rivers in the boreal forest.

SELECTED SPECIMENS. **Alaska:** Eastern Pacific Coast district: Glacier Bay, _Cooper 166_ (US), _200_ (NA); Skagway, _Eastwood 793*_ (A). **Yukon:** MacRae, _Gillett 3529*_, _3530*_ (DAO), Carcross, _7788*_ (DAO); L. Bennett, _Seale_, June 1898*, (DS). **British Columbia:** Haines Rd., Mi. 81, _Taylor, Szczawinski, & Bell 1383_ (UBC), Mi. 98, _973_, _975_ (DAO, UBC); Atlin L., _Aitken 18*_, _19*_, _20*_ (DAO); _Eastwood 655*_, _657*_ (A, US); Atlin, _Setchell & Parks 10*_ (NA); Bennett, _Malte 122171*_ (A); _Mitchell 177*_ (DAO), _178*_ (DAO, UBC); Vista, _Walpole 1273*_, _1275*_ (US); Azouzetta L., _Calder, Savile, & Ferguson 14092_ (DAO); Caribou, Flying U. Ranch, _Eastham, 11528_ (NA, UBC); White Pass, _Gillett & Mitchell 3669_ (DAO); Anahim L., _Hatter 7_, Kleena, Kleene, _12_ (NA, UBC); Mt. Robson Prov. Pk., Berg L., _Jenkins 7267_ (DAO); Mt. McLean, near Lillooet, _Macoun 97772_, Skeene R., mountains south of Hazelton, _97807_ (A, GH, NA); head of Dease L., _McCabe 8694_, _8820_ (NA); Yoho Nat. Pk., Mt. Stephen, _McCalla 9598A_ (UBC); Cassiar Dist., Thutade L., _Preble & Mixter 678_ (US); Mt. Selwyn,, _H. Raup & Abbe 3763_ (A, MIN, NY), _4173_ (A, NY); Watson L., _H. Raup & Correll 11062_, Beaton R., _10258_, _10259_ (A); Summit Pass, Alaska Hwy., _Taylor, Szczawinski, & Bell 101_ (DAO, UBC); Elk R. valley, 27 mi. N. of Natal, _Weber 2261_ (GH, NA, NY, UBC. **Alberta:** Rocky Mts., near Bow R., _Bourgeau_, 1858 (GH); Highwood district, Cataract Cr., _Brinkman 3261_ (US); Mercoal, _Malte & Watson 116892_ (A, GH, NA); Jasper Nat. Pk.: Maligne L., _Brown 1193*_ (GH); Mt. Cavell, _Fraser 9*_, _13*_ (NA); bank of Athabasca R., _Jack 2574*_ (A, NA); Signal Mt., _2610*_ (A), trail to Whistlers Mt., _2695*_ (A) _2704*_ (A, NA); Beauvert L., _Macoun 95382_ (A, GH, NA, NY), _126*_, _127*_ (A), Cabin L., _95763*_, Goat Mt., _95782*_, Pyramid L., _95785*_, _95786*_, _95788*_, Shovel Pass, _95795*_, Goat Mt., _95796*_ (A, NA), _95797*_, Brule, _99*_, _109*_ (A), _111*_ (A, DAO), Maligne L., _116*_, _117*_ (A), Old Man Mt., _133*_ (A, DAO), Maligne-Athabasca, _138*_ (A); Sunwapta Pass, _Moss 4892*_ (NA);

below Mt. Cavell, *A. & R. Nelson 4854** (NA); Angel Gl., Mt. Cavell, *Scamman 2441**, Medicine L., *2520**, mountain above Maligne L., Pk.: Lake Louise, *Eggelston 21756* (US); *Jack*, 10 Aug. 1904 (A); *2618**, *2619** (GWA), Columbia Ice Field, *2745** (GH); Banff Nat. *Macoun 68894* (GH, NA, NY); Castlemount Ranger Sta., *Malte & Watson 116769* (A, GH, NA); Bow summit, *Weber 2467* (GH, NA, NY); Waterton Lakes Nat. Pk., Chief Mt. Inter. Hwy., *Breitung 15806* (NA, NY); Wood Buffalo Pk., Pine L. district, *H. Raup 2136* (US). **Montana:** Glacier Nat. Pk.: *Jack 1539**, *1540** (A); Gunsight Pass, *H. & V. Bailey 1533** (NA); Many Glacier, *Jack 2056**, trail from Many Gl., to Swiftcurrent Pass, *2132**, Cracker L., *2162** (A), Piegan Pass, *2211** (A, US); *Maguire 680** (NA); *Standley 17456** (US); Blackfoot Gl., *Jones*, 1 Sept. 1909* (NY); Granite Pk., Chalet, *Standley 16249** (NA, US), Iceberg L., *16442**, Swiftcurrent R., *16509** (US), trail from Many Gl. to Piegan Pass, *17450** (NA); Carbon Co.: Beartooth Mts., *Cronquist 7997* (DAO, DS, GH, MIN, NY); 17 mi. south of Red Lodge, *Rollins & Muñoz 2832* (DS, GH, NA, US). Fergus Co.: Big Snowy Mts., *Hitchcock & Muhlick 11986* (DS, GH, NA, NY). **Wyoming:** Albany Co.: Nash's Fork, *A. Nelson 7831* (RM); La Plata Mines, *E. Nelson 5166* (RM). Fremont Co., Christina L., *Porter 5231* (DS); Lincoln Co., Dead Mans Pk., *Williams 1289* (NA, NY, RM); Park Co., Clay Butt, *Porter & Rollins 5872* (RM); Sheridan Co., Big Goose Cr., *Tweedy 216* (US); Sublette Co., near Green R. Lake, *E. & L. Payson 4570* (GH, NA); Teton Co.: Hoback Canyon, *Wehmeyer, Martin, & Loveland 5467* (NY); Yellowstone Nat. Pk., Amethyst Mt., *Knowlton*, 18 Aug. 1887 (US). **Colorado:** headwaters of Clear Cr. and alpine ridges east of "Middle Park", *Parry 341* (GH, NY); Boulder Co.: Redrock L., *Ramaley & Robbins 5071; Smith 2272* (NA). Chaffee Co.: Cottonwood Canyon Rd., *Beetle 2173* (GH). Clear Creek Co.: Berthoud Pass, *Clokey 3752* (GH). Custer Co.: Brush Cr., *Cockerell*, 1899 (NY). Delta Co.: Grand Mesa, *Maguire 12756* (NY). Eagle Co.: Tennessee Pass, *Eggleston 11783* (US). El Paso Co.: Pikes Pk., *Bacigalupi 771* (GH). Garfield Co.: Newcastle, *Harrington 4317* (NA). Grand Co.: near Eldora, *Demaree 38706* (NA). Gunnison Co.: Virginia Basin, *Langenheim 298* (NA); Blain Basin, *Levi 3* (GWA). Gunnison-Pitkin Co. line: E. Maroon Pass, *Levi 6* (GWA). Hinsdale Co.: Slum Gullion Pass, *Levi 1* (GWA). Jackson Co.: mts. west of Cameron Pass, *Williams 2435* (US). Larimer Co.: Trail Ridge, Rocky Mt. Pk., *Smith 2239*, *832* (NA), *1779* (GWA). Lake Co.: Leadville, *L. & E. Kelso 4886* (DAO). Mesa Co.: top of Grand Mesa, *R. Schneider 837* (NA). Montezuma Co.: LePlata Mts., Mt. Hesperus area, *L. Kelso 6103* (DAO). Ouray, Co.: Ouray, *Kiltz K-784* (A). Park Co.: ridge to North Star Mt., *Weber 7140* (DAO). Routt Co.: Ethel Pk., *Gooding 1893* (NA). San Juan Co.: Silver-ton, *Tweedy 271* (US). Summit Co.: south of Climax, *Durrell 12* (NA). Teller Co.: near Pikes Pk., *Shantz*, 20 July 1903 (NA). **Utah:** Mt. Parry, *A. Gray*, 1872 (GH). Cache Co.: Bear R. Range, Mt. Naomi, *Maguire, Hobson & R. Maguire 14144* (NA). Duchesne

Co.: Uinta Basin. Mt. Emmons, *Grahm 8518* (NA, US). Iron Co.: Dixie Nat. Forest, Cedar Breaks Canyon, *Maguire 17561* (NY). Kane Co.: northwest of Orderville, *Maguire 18831* (NA). Rich Co.; Bear R. Canyon, *Watson 1100* (GH, US). Salt Lake Co.: Big Cottonwood Canyon, *Garrett 1595* (US). Summit Co.: Uinta Mts., Henry Fork Cr., *B. Maguire, Hobson, & R. Maguire 14361* (NY). Utah Co.: trail to Mt. Timpanogos, *Maguire 17485* (NY). Wasatch Co.: near Midway, *Carlton & Garrett 6707* (GH). **New Mexico:** Castilla Valley, *Wooton*, 4 Sept. 1913 (NY, US). Colfax Co.: Baldy Pk., *Standley 14364* (US). Taos Co.: Taos Mt., *Bailey 884, 885* (US).

SELECTED SPECIMENS OF THE FERRUGINOUS FORM, ROCKY MOUNTAIN PHASE

Alaska: Clearwater R., *Argus 827* (GWA, RM). **British Columbia:** Beaton R. Crossing, *Taylor, Szczawinski, & Bell 64* (DAO, UBC); Alaska Hwy., Mi. 347 and Liard R., *H. Raup & Correll 10998, 11001, 11005* (A); Liard Hot Springs, *10907* (A). **Alberta:** Calgary, *Macoun 94426* (NA); Jasper Nat. Pk.: *Jack 2749* (A, NA); Mt. Cavell, *Ledingham 49-645** (DAO); Athabasca R., *Macoun 95377* (A, GH, NA, NY); Moose L. dist., *Raup 8122* (GH), *8125* (CAN); Edmonton, *Turner 1299, 1782* (A, DAO, NA). **Manitoba:** Otterburne, *Bernard 58/398* (MTSM); Riverton, *Scoggan 9024* (CAN); York Factory, *6062* (CAN, MIN), *6088A* (CAN); Churchill: *Argus 494-58*, 496-58*, 517-58*, 518-58*, 519-58**, Farnworth L., *459-58*, 456-58**, Bird Cove, *490-58** (GH, GWA), Warkworth Cr., *Gillett 2154* (DAO); Herriot Cr., Churchill R., *Argus 301-58* (GH, GWA). **Saskatchewan:** McKague, *Breitung 73* (A, DAO, NA, NY), *162* (A, DAO, NY), *174* (A, DAO, NA, NY), *542* (A); Prince Albert, *Fraser 1* (NA); Stony Rapids, *Maini 314* (GWA, SASK); Hasbala L. region, *Argus 857-62* (DAO, GWA, SASK). **Yukon:** Canol Rd., Mi. 136-138, *Porsild & Breitung 9776* (GH); Watson L., east end, *H. Raup & Correll 10921, 11050, 11061* (A). **Northwest Territories:** Hay R. settlement, *Lindsey 128* (CAN); Enterprise-Mackenzie R. Hwy., Mi. 56, *Thieret & Reich 4796*, Mi. 11, *4830* (F, GWA).

EASTERN PHASE. FIGS. 6, 6a, 40-45

Principal Synonymy. *Salix cordifolia, S. callicarpaea, S. cordifolia* var. *callicarpaea, S. labradorica, S. glauca* var. *stenolepis, S. glauca* ssp. *callicarpaea*, and in Greenland *S. anamesa*.

Amplified Description. Shrubs prostrate to 5 feet tall, averaging from 2 to 3 feet tall. Branchlets sometimes white-tomentose in the north and west but finely pubescent in the east. Branches often glabrous, in some areas up to 30 per cent with pruinose branches and buds. Leaves commonly elliptical, or narrowly so, to oval or obovate. Leaf-apex acute to obtuse, depending somewhat on the general leaf-shape. Leaf-base obtuse to rounded or sometimes cordate in the east. Leaf-size 2-5 cm. long. Petiole longer in relation to leaf-length than in the Western phase. Leaves usually glabrate above and thinly pubescent below, dense pubescence uncommon, margin entire, glands near the base in some. Stipules present but not prominent and rarely exceeding 1 mm. in length. Pistillate aments short, 2-5 cm. long in fruit. Ovaries white-tomentose becoming glabrescent to thinly pubescent in age. Pedicel from 0.25 to more commonly 0.5-1 mm. long. Style often short and entire, some divided part way to the base, reddish in preanthesis and yellow-green in anthesis.

FIGS. 40-41. Representative specimen of the Eastern phase of *Salix glauca. Fernald & Collins 212*, 5 and 12 Aug. 1906, Tabletop Mt. (Mt. Jacques Cartier), Quebec. FIG. 40. General view, note persistent ament of previous year on branch in upper center. FIG. 41. Closeup of pistillate ament.

FIGS. 42-45. Representative specimens of the Eastern phase of *Salix glauca* from Churchill, Manitoba. FIG. 42-43. Staminate specimen, *Argus 4S*, 15 July 1962. FIG. 42. General view, note pubescent branchlet and shiny, glabrescent branch. FIG. 43. Closeup of staminate ament. FIG. 44. An erect specimen of *Salix glauca*, 3.5 feet tall, growing in the lee of the outcrop ridge at Churchill, Manitoba (*Argus 34S*). FIG. 45. A prostrate individual of *S. glauca* growing on the outcrop ridge a short distance from the individual in FIG. 44 (*Argus 501-58*). See Figs. 6 & 6a for pistillate specimen from Churchill, Manitoba.

Distribution (Map 2). The Eastern phase of *Salix glauca* occurs from southern Keewatin and northern Manitoba southward along the coast of Hudson and James Bays into northern Quebec, Labrador, and Island Newfoundland. It extends northward into southeast Baffin Island and Greenland, and southward to the southern coast of Quebec, the Mingan Archipelago, Anticosti Island, the Shickshock Mts. of the Gaspé Peninsula, and St. Paul Island. The influence of the Eastern phase extends westward into the Great Slave Lake region where it intergrades with the Western and Rocky Mountain phases.

Discussion. The Eastern phase of *Salix glauca* has long been regarded as a distinct species, *S. cordifolia* (usually as the variety *callicarpaea*). All the evidence I have been able to accumulate supports the conclusion that it is best regarded as being conspecific with *S. glauca*. However, if its chromosome-number is shown to be consistently different from *S. glauca*, as suggested in the section on cytology, it may have to be reassigned specific rank.

The Eastern phase is relatively homogeneous throughout its entire range, especially east of Hudson Bay. This is in contrast to the other phases which vary widely and contain scattered individuals morphologically resembling other phases. I have not seen a single specimen from east of Hudson Bay that could be assigned to one of the other phases. In northern Manitoba the Eastern phase, although the dominant form, shows an increasing influence of the Rocky Mountain phase. This influence is reflected in a general diminution of leaf, stem, and capsule-pubescence, slightly longer pedicels and petioles, and the occurrence of occasional ferruginous leaf-pubescence. The influence of the Western phase is noted in central Keewatin and to the west where oblanceolate leaves, occasional villous-sericeous leaf-pubescence, and longer stipules and aments begin to appear.

At Churchill, Manitoba, *Salix glauca* is an ubiquitous species occurring in most habitats and is dominant in several. Although morphological variation in the species in different habitats is not evident, variation due to microenvironmental differences, such as protected niches, or south-facing exposures, is striking (compare Figs. 45 & 44, the former is a prostrate individual growing on the outcrop ridge, and the latter is an erect shrub growing in the lee of the same outcrop ridge). It is under such microenvironmental conditions that forms referred to the Western phase by some taxonomists have been produced (C. R. Ball, *in* Ritchie, 1956).

East of Hudson Bay the Eastern phase occurs throughout the region roughly corresponding to the forest-tundra transition and the artic tundra of eastern Canada. In this area leaf-pubescence is highly variable, ranging from densely pubescent on both surfaces to almost completely glabrescent. These extremes are connected by a continuous array of intermediates. In some areas (especially James Bay) densely pubescent specimens suggest hybridization with *Salix brachycarpa.* Similarly, pruinose stems found in about 20-30 per cent of the specimens from northern Quebec and Baffin Island suggest hybridization with *S. arctica.* However, in neither case is the evidence unequivocal. Pruinose stems may have been derived through hybridization and introgression with *S. planifolia* as well as *S. arctica,* and such characteristics may represent introgression from "ancient" hybridization which is no longer going on and the characteristics may now be fully integrated into the species. On Baffin Island *Salix glauca* and *S. arctica* appear to converge in their morphology, and although hybrids may occur they are virtually impossible to identify because of being so similar to their putative parents. This problem of hybridization and the recognition of hybrids is acute in Greenland as well as on Baffin Island and critical field studies are very much needed. Cytological information may also be of value because *S. arctica* is tetraploid and *S. glauca* is either hexaploid or octoploid.

Along the Labrador coast *Salix glauca* exhibits very wide phenotypical variation. Shrubs range from prostrate to 4-5 feet tall and in some specimens broad leaves with subcordate bases occur. However, in general the shrubs are 1-2 feet tall and the leaves elliptical-oval and obtuse at both ends.

On Newfoundland, numerous specimens with small oval to suborbicular leaves of the "*macounii*" or "*eucycla*" type have been collected. These leaf types occur as prostrate individuals and have been collected also from the Strait of Belle Isle coast and other localities on the western coast. There are also erect forms and various intermediates in this area but there seems to be a definite tendency toward prostrate, small-leaved forms. In this area the specimens show a closer morphological resemblance to those from the Labrador area than to those from the Gulf of St. Lawrence. However, in spite of this considerable variation in vegetative structure there is very little variation in their reproductive structures.

The Eastern phase does not seem to occur in the spruce-fir forest of southern Quebec but appears only along the coastal fringe which experiences a rigorous environment apparently unfavorable for tree growth. It is fairly common on the Mingan Archipelago but has been collected from only one locality on Anticosti Island. The specimens I have seen from this general area are thinner-leaved than usual and have very short pedicels.

A southern outlier of the Eastern phase in the Shickshock Mts. probably represents an isolated remnant of what was once an extensive population in eastern North America. It has been collected on Mt. Logan, Mt. Jacques Cartier (Tabletop Mt.), and on Mt. Albert. In the latter locality it is rare and causes some confusion with *Salix brachycarpa* which tends to vary in the direction of *S. glauca* in favorable habitats and may even hybridize with it.

Ecology. The Eastern phase of *Salix glauca* is the commonest willow along the east coast of Hudson Bay (Hustich, 1950), and throughout its entire range in eastern Canada. It is principally a species of the forest-tundra transition, extending into the adjacent tundra and the boreal forest. In the forest-tundra of Quebec and Labrador it occurs in *Picea glauca* forests and *Picea mariana*, *Larix laricina* muskegs, in meadows, and on sandy and gravelly beaches, and river margins. In Newfoundland it is common along the sea cliffs both on quartzitic cliffs and the serpentine tableland (Bonne Bay). It also occurs in the lichenheath tundra, spruce thickets, and on dry limestone barrens.

In the region of the Hudson Bay lowlands it occurs on river banks, coastal meadows and gravel ridges. It is most commonly collected from river flood plain thickets, and gravel or clay river banks. At Churchill, Manitoba, it occupies a variety of habitats from the tundra of the outcrop ridge to dense willow thickets along the Churchill

River, and in both *Picea glauca* and *Picea mariana, Larix laricina* forests. It is much less common in the forests than in the tundra or along water courses.

In the Gulf of St. Lawrence area it occurs principally in calcareous situations such as limestone-shingle beaches, calcareous slopes and cliffs, but it also occurs on granitic cliffs. It is an alpine species on the Gaspé Peninsula where it occurs only on the mountains in alpine and subalpine meadows, brooksides, and on cliffs and talus slopes. On Mt. Albert it occurs in both serpentine and amphibolite situations.

SELECTED SPECIMENS. **Northwest Territories:** District of Keewatin: Ennadai L., *Brown 1344* (CAN); Plover L., *Clarke 00757* (CAN); Nueltin L., *Harper 2500* (CAN, MIN, NY); Lower Thelon R., *Lawson 71* (CAN); Dubawnt R., *Oldenburg 46-1571, 46-1576* (GH); *Baffin Island:* Frobisher Bay, *Calder 2054** (DAO, US); *Potter 8669** (NA); *Sewall 280** (GH); Pangnirtung, *Dutilly 9464A** (NA); *Malte 118696*, 118702** (US), *118807*, 118808** (NY), *118701** (NY, US); *Sanson 7** (NA); Lake Harbor, *Dutilly 9136*, 9142*, 9143** (NA); *118697*, 118709*, 121033** (NA, NY), *118698*, 118707*, 118810*, 120308*, 120324*, 121031** (NY, US), *126876** (GH), *120329** (NY), *120297* (US); **Islands of James Bay:** South Twin Isl., *Baldwin 1621;* Solomons Temple Is., *1670* (GH); Akimiski Is., *Dutilly & LePage 15597* (GH); **Islands of Hudson Bay:** Long Is., *Dutilly & LePage 14214* (GH); Christie Is., *Dutilly, O'Neill, & Duman 87861* (NA, US); Cairn Is., *E. & L. Abbe, & Marr 3481** (DS, MIN), *3540** DAO); *E. & L. Abbe 3540*, 3541*, 3037** (MIN). Manitoba: Nueltin L., *Baldwin 2249* (GH), *2250* (CAN, GH); Churchill, *Argus 4-S, 34-S, 196-58, 336-58, 364-58, 414-58*, 431-58*, 434-58*, 436-58*, 438-58*, 457-58*, 462-58*, 465-58*, 470-58*, 471-58*, 482-58*, 485-58*-488-58*, 503-58*, 507-58*-509-58, 523-58, 524-58** (DAO, GH, GWA, RM); *Macoun 79159* (A, GH, NY); York Factory, *Scoggan 5942* (CAN, MIN); Nelson R., *6341, 6360* (CAN, MIN). **Ontario:** Moosonee, *Dutilly & LePage 12075* (GH); Cape Henrietta Marie, *31245* (NA); jct. of Fawn R., and Mink Cr., *Moir 722* (CAN, GH); jct. of Fawn R. and Poplar R., *863* (GH); mouth of Severn R., *1510* (CAN, GH); mouth of Lowaski R., *Smith 42* (NA, US). **Quebec:** Great Whale R., *Doutt 2528** (NA); *Savile 227*, 229*, 230*, 275*, 276*, 388** (DAO), *417** (DAO, US), *418*, 612*, 631*, 687*, 755** (DAO); Richmond Gulf, *Dutilly & LePage 13120*, 13213** (GH); *E. & L. Abbe 3303** (MIN); Wiachewan R., *3401*, 3402** (MIN), *3385** (MIN, RM); *E. & L. Abbe, & Marr 3317** (DAO, MIN, US); mainland south of Cairn Is., *3461** (MIN, US); Port Harrison, *Malte 127040* (GH, NY, US); Kogaluk R., 20 mi. from bay, *Rousseau 293* (DAO); between Tashwak L. and Payne L., *628* (DAO, US), *778* (DAO); Payne L., *Rousseau 892* (GH), *981* (DAO); Wakeman Bay, *Gardner 719* (GH, NA); *Malte 126917* (GH, NY, US); Ft. Chimo, _Calder 2276_ (DAO, RM); George R., various localities, _Rousseau 531*, 597*, 654*, 659*, 694*, 697*, 714*, 774*, 800*, 804*, 876*, 878B*, 902*, 903*, 921*, 935*, 998*,1089*_ (DAO), _598*, 878A_ (DAO, GH); Korak R., 70 mi. from bay, _860_ (NA); Mollie T. Lake, _Harper 3758_ (MIN); Knob L., _Hustich 450_ (GH); St. Lawrence region: Mingan Is., _Brunel 149*_ (GH); _St. John 90836*, 90838*, 90846*_ (GH); _Victorin & Germain 18915*, 18927*, 25187_ (GH, US), _18916*, 18923*, 18932*, 25932*_ (GH), _18926*, 25188_ (GH, NY), _25184*, 25922*, 25925*_ (A, GH), _25183*_ (A, GH, US), _18925, 18930*, 18931_ (GH, NY, US), _18922*_ (DS, GH, NY, US), _18924*_ (DS, GH, NY); Anticosti Is., Bay St. Clair, _Victorin 4351_ (A, GH, NY, US); Strait of Belle Isle, Blanc Sablon, _Fernald & Long 28031*_ (A, GH); _Fernald & Wiegand 3223*_ (GH), _3225*_ (A, GH, NA), _3224*_ (A, GH, NA, NY, US); _Griscom 1*_ (GH); Gaspé Pen., Mt. Auclair, _Louis-Marie, et al. 34402_ (GH, NA); Mt. Blanc, _Pierce & Hodge 9A_ (GH, NY); Mt. Logan, Lévesque _48004_ (DAO, NA); alpine pass bet. Mts. Logan and Fortin, _Fernald & Pease 25008_ (A, GH, NA, NY, US); Pease Basin, bet. Mts. Logan and Pembroke, _Fernald, Griscom, & Mackenzie 25673_ (A, GH, NA, NY); Tabletop Mt., _Fernald, Dodge & Smith 25683_ (A, GH, NA, NY, US); _Fernald & Collins 212_ (A, GH, MIN, NY, US); Mt. Albert, _Collins & Fernald 63_ (A, GH, MIN, NY, US); _LePage 3898_ (NA, RM). **Newfoundland:** Labrador: Komaktorvik Fjord, _Dutilly, O'Neill, & Duman 7865_ (NA); Saglek, _Gillett 8568_ (DAO, US); Crater L., north Hebron R. valley, _8729_ (DAO, RM, US); Sumavik, _Bartlett 18*_ (US); Cape Mugford, _Dutilly, O'Neill, & Duman 7765*_ (NA); _Gardner 378*, 379*_ (NA), _392X*_ (DAO, NA), _39-439*_ (GH, NA); _Potter & Brierly 8566*_ (NA); Nain, _Bishop 243a*_ (GH); _Walker 1113*_ (NA); Davis Inlet, _Dutilly, O'Neill, & Duman 7610*_ (NA); Windy Tickle, _7493*_ (NA); _Potter & Brierly 8617a*_ (NA); Hopedale, _Dutilly, O'Neill, & Duman 7420*, 7428*_ (NA); _Potter 8644*_ (NA); _Potter & Brierly 8619*_ (NA); Flint Is., near Port Manvers, _Bryant 94*_ (GH); Port Manvers, _Dutilly, O'Neill & Duman 7650*, 7669*_ (NA); _Potter 8658*_ (NA); _Walker 499*_ (NA); Jack Lane Bay, _Dutilly, O'Neill, & Duman 7564*_ (NA); Domino, _Gardner 82_ (GH, NA); Gready Is., Gready Harbor, _Bryant 90_ (GH); Rodney Mundy Is., Indian Harbor, _Abbe & Hogg 243_ (A, GH, MIN); Kikkivitak Is., _Abbe 249*_ (A, GH); Battle Harbor, _240_ (A, GH); Strait of Belle Isle, Forteau, _Fernald & Wiegand 3209*-3714*, 3220*_ (GH); _Long 28029*_ (GH); _Waghorne 4*_ (A), _7*_ (MIN, US); Island Newfoundland: St. Anthony, _Abbe 238_ (GH, MIN); Trinity, _Ayre_, Aug. 1935 (GH); Highlands of St. John, Doctor Hill, _Fernald & Long 27977, 27978_ (A, GH); Flower Cove, _Fernald, Long, & Dunbar 26569_ (A, GH, NY), _26570_ (A, GH); Bonne Bay, _Fernald, Long & Fogg 1612_ (A, GH, NA, NY); _Fernald & Wiegand 3230_ (A, GH, NA, NY); Ingornachoix Bay, _3219_ (GH); Cape St. George, _Mackenzie & Griscom 11024_ (DS, NY, US). **Nova Scotia:** St. Paul Is., _Eskine 53810_ (DAO); _Perry & Roscoe 170_ (A, GH, NY).

SELECTED SPECIMENS FROM TRANSITIONAL AREA BETWEEN THE WESTERN, EASTERN, AND ROCKY MT. PHASES

Northwest Territories: District of Mackenzie: Coppermine, _Findlay 65, 218_ (DAO, RM, US); Norman Wells, _Cody & Gutteridge 7441_ (DAO); Ft. Good Hope, _Preble 330, 332_ (US); Great Bear L., Port Radium, _Cody 2790*_ (DAO), Gunbarrel Inlet, _2827*, 2828*_ (DAO); Sawmill Bay, _Corcoran 15*_ (DAO); Leith Pt., _Preble 291*, 292*, 293*, 294_ (US); Ft. Franklin, _Richardson 58_ (NY), _70_ (GH), _397_ (A), Mackenzie R., Ft. Franklin?, _72, 73_ (NY), _76_ (A, NY), _399_ (GH); Port Radium, _Shacklette 2752*, 2881*_, Leith Pen., _2955*, 3081a*, 3100*, 2838*_, McTavish Arm, _2792*, 3200*_, Hunter Bay, _3211, 3212_ (NA, US). Indin L., _Cody & McCanse 3357_ (DAO); Great Slave L., _Snare R. Power Sta., Cody 2627*_ (DAO, US), Yellowknife, 7 Aug. 1949* (DAO); _Cody & McCanse 2403*_ (DAO), _2404*_ (DAO, MIN), _2493*_, Harditsy Is., _2907*, 2920*_ (DAO); Moraine Pt., _Lewis 485*_, Long Is., _849*_, Barabant Is., _2907*, 2920*_ (DAO); Moraine Pt., _Lewis 485*, Long Is., 849*_, Barabant Is., _1020*_ (DAO); Yellowknife, _Morrison 17*_ (NA); Ft. Resolution, _Preble 194, 198_ (US); Ft. Providence, _Preble & Cary 42*_ (US); _Thieret & Reich 5027, 7748_ (F, GWA); Ft. Rae, _E. & A. Preble 138*_ (US), Ft. Resolution, _141_ (A, NA, US); Gros Cap Is., _Reeder S-1788*_ (DAO); Caribou Is., _Seton & Preble 43*_ (NA); Kakisa L. Rd., _Thieret & Reich 4728, 4637, 4963;_ Horn Mts., _5802*, 5867*, 5927*, 5932*_ (F, GWA), Mackenzie R. near Trout R., _Cody & Matte 8636*_ (DAO); Enterprise-Mackenzie R. Hwy., Mi. 33, _Thieret 4316_ (F, GWA); Muskox L., _Chillcott 134, 166, 178_ (DAO). District of Keewatin: Chesterfield, _Gardner 487_ (GH). **Alberta:** Ft. Smith, _Cody & Loan 3852_ (DAO, MIN, RM); Moose (Eight) L. dist., _H. Raup 2130_ (GH, NY, US), Pine L. dist., _2136_ (GH, US); near Heart (Raup) L., _2139_ (GH), Caribou Mt. Plateau, _2140_ (GH, NY, US); L. Athabasca, Sand Pt., _H. Raup & Abbe 4528_ (GH, MIN, NA, NY). **Saskatchewan:** Lake Athabasca: Charlotte Pt., _H. Raup 6178*, 6181*, 6182*, 6184* - 6186*_ (GH, NA, NY), _6196*_ (GH, NA), _6223*_ (GH), _6297*_ (GH, NA, NY), _6354*_ (GH), _6355*, 6356*, 6357*_, Cornwall Bay, _6458*, 6459*_ (GH, NA, NY), _6459a*_ (GH), _6460*-- 6463*,6569*_ (GH, NA, NY), _6513*_ (GH, NA); Hasbala Lake region: "Quillwort" L., _Argus 849-62, 1031-62, 1034-62_ (DAO, SASK, GWA), _854-62_ (DAO, GH, GWA, SASK).

SALIX GLAUCA IN GREENLAND

In the early stages of this study _Salix glauca_ in Greenland was not to be included because of its known complexity and the need for special field study. However, as an understanding of the North American _S. glauca_ developed it became apparent that a general treatment of the species in this area would be of value. This change in plans has made it impossible to examine all of the material available from this area, particularly that in European herbaria, nor has it been possible to typify all of the infraspecific taxa applied to this species in Greenland. This work, although important, must be left to the future.

Salix glauca in Greenland has been treated taxonomically in three ways: 1) the species is sometimes recognized as consisting of several infraspecific taxa based on its highly variable leaf-pubescence, leaf-shape, and habit (Lange, 1880, *et al.*) ; 2) the species may be regarded as rare and the bulk of the material identified as double or triple hybrids, involving *S. glauca, S. arctica* and/or *S. arctophila* (Floderus, 1923) ; and 3) the species may be recognized as widespread and highly variable but treated in a broad sense as *S. glauca* s.l.

The recognition of hybrids was common during the 1930's under the strong influence of Floderus. Seidenfaden (1933) deserves special mention because of his attempt to combine anatomical and morphological characteristics to understand *S. glauca, S. arctica, S. arctophila* and their putative hybrids. Although I have not yet examined all of the anatomical characteristics he used, those that I have studied are either too similar in the various taxa to be of diagnostic value (e.g. the number of cells in a tangential view of medullary rays) ; or apparently inaccurate (e.g. the size of epidermal cells). He reports that *S. arctica* and *S. arctophila* have large epidermal cells (400-900 per square mm.) contrasted with the small cells of *S. glauca* (2000-4000 per square mm.). My work shows that *S. glauca* and *S. arctica* are very similar in cell size (2000-3500 cells per square mm.) ; compare Figs. 3-8 & 3-9 with Fig. 4. The largest cells noted in *S. arctica* were only 1500 cells per square mm. (in *Heusser 4T* from Southeastern Alaska (GWA)).

However, through the use of combined anatomical and morphological characteristics Seidenfaden classified all his material into 5 levels of hybrids from almost pure *Salix arctophila*, through three degrees of hybrids to almost pure *S. glauca* (*S. arctica* was not present in the area he studied, south of 64°N.). The improbability of this treatment was even recognized by its author who noted that, "A division into the above-mentioned five types will, of course, always be greatly subjective, and a later more thorough investigation will probably arrive at a different result."

In 1938, T. W. Böcher expressed some concern about the treatment of *Salix* as hybrids and suggested that the hybrids be verified experimentally. However, he considered *S. glauca* to be rare and ordinarily was involved in hybridization. He did note that pure *S. glauca* occurred in scrub or form scrub and cited as authority for this Hartz, Kruuse, and Rosenvinge, all pre-Floderan botanists. In 1952, his view changed somewhat and he regarded the hybrid *S. arctophila × glauca as* "ill-founded". He recognized *S. glauca* as "a variable and critical group", and referred the glabrous form to *S. glauca* ssp. *callicarpaea* and the hairy form to *S. glauca* (*see* discussion of synonymy of *S. glauca*).

This trend back to recognizing *Salix glauca* in a broad sense and down-grading hybridization was followed by Polunin (1943) who noted *S. glauca* as being common and "extremely and tiresomely variable". He not only disagreed with the general recognition of *Salix* hybrids but stated that *S. arctophila* and *S. glauca* seem not to hybridize even when growing in the same marsh. Polunin also pointed out the resemblance of the Greenland *S. glauca* to the species in eastern Canada. This general interpretation was expanded by Lagerkranz (1950), who proposed to call the Greenland species *S. callicarpaea*. Later Böcher (1952) proposed the combination *S. glauca* ssp. *callicarpaea*.

I regard *Salix glauca* as being widespread in western Greenland, less common but present in east Greenland, and having the same intraspecific variation as found in the Eastern phase of the species. *Salix glauca* in Greenland is considered to be more closely related to the Eastern phase than to the species in Europe or Western America. Hybrids involving *S. glauca, S. arctica,* and possibly other species probably occur in this region, but at best they are difficult and identification is highly subjective. I have been very careful about identifying specimens as hybrids but some material appears unmistakeably to be the hybrid *S. arctica × glauca*. I have been unable to detect *S. arctophila* in any of my material for it differs from *S. arctica* only subtly and it is impossible to recognize putative hybrids from specimens alone.

In "pure" *Salix glauca*, leaf-indument varies from densely pubescent on both sides to almost glabrate. I have not been able to associate this with habitat, although Böcher (1952) relates the densely pubescent-leaved forms to sunny exposures and the glabrescent-leaved forms to moister places on northern slopes or near running water. The size and shape of leaves also vary widely, possibly due to different environments. The branchlets are more or less pubescent, becoming glabrate in age. Many of them are pruinose, a characteristic reminiscent of *S. arctica*. The styles are entire or divided almost to the base; however, the majority show little or no division. The bracts of the flowers are often darker brown than in *S. glauca* and may bear the straight pubescence of *S. arctica,* further suggesting introgression with that species.

The habitats occupied by *Salix glauca* in Greenland are very diverse, similar to the species in eastern Canada. An account of its ecology is given by M. P. Porsild (1920) who notes that it forms copses in places providing sun and moisture during the summer. "Thus often on the sunny side of rocky walls, these lying sheltered from the wind. Besides it is always present in the heath-vegetation, both in the dry part and in the moist. It is to be found in bogs right down to the lake shore and is sometimes growing in the most dry and barren places, dunes, gravel among boulders and stones, on rock-ledges and in crevices." That its occurrence in diverse habitats may account for its wide phenotypical variation has been suggested by M. P. Porsild (1920), Seidenfaden (1933), *et al.*

SELECTED SPECIMENS. **West Greenland:** Tasermiut Fjord, *A. & M. Porsild,* 27-28 July 1925 (GH, NY, US); Godthaab, *Lagerkranz,* 30 August 1936 (A, RM); Ivigtut, *Dutilly 9483* (NA); Neria, *Eugenius,* 13 July 1925 (GH, NY, US); Ameralik, *Lagerkranz,* 26 August 1936 (A, RM); Söndre Stromfjord, *Erlanson 2376* (GH, NA); Ikinea, *M. Porsild 3622* (GH); Godhaven, *Bartlett 63* (GH, US); *Diske, Warming & Holm, 20 July 1884* (DAO); Ritenbank Flor, *Lagerkranz,* 18 August 1934 (RM); Nugsuak Pen., Patut. *Erlanson 3329* (NA); Kingigtok, *3287* (CAN); Umanaq, *Enander,* 8 July 1921 (A, GH); Cape York, *Wetherill 209, 213, 214* (GH). **East Greenland:** Angmagssalik Fiord, Kungmuit, *Bartlett 448* (US); Angmagssalik, *Lagerkranz,* 8 August 1946 (MIN.).

Salix brachycarpa Nuttall, N. Amer. Sylva **1**:69. 1842

Salix brachycarpa is restricted to North America and is treated here as consisting of three infraspecific taxa, ssp.

brachycarpa, ssp. *niphoclada,* and ssp. *niphoclada* var. *fullertonensis.* Each of these infraspecific taxa has been regarded, in the past, as a separate species. However, some taxonomists have favored the reduction of one or another of them to infraspecific rank. Rydberg (1899) regarded *S. niphoclada (S. brachycarpa* ssp. *niphoclada)* as most closely related to *S. stricta (S. brachycarpa* ssp. *brachycarpa).* This view was supported by Ball (1934) when he described *S. brachycarpa* var. *mexiae,* which was recognized later to be the same as Rydberg's *S. niphoclada* (Raup, 1959). This judgment of a close relationship between *S. brachycarpa* and *S. niphoclada* has not been concurred in by all taxonomists (*see* Hultén, 1943, and Raup, 1959), but no one has presented a clear case against it.

Some of the confusion regarding the position of *Salix brachycarpa* ssp. *niphoclada* in the *S. glauca* complex has stemmed from the widespread hybridization between ssp. *niphoclada* and *S. glauca* in parts of northern Alaska. This hybridization is thought to have resulted in a modification of ssp. *niphoclada,* in that area, in the direction of *S. glauca.* Some authors were led to regard it as a subspecies of *S. glauca* (Wiggins and Thomas, 1962). This view is unsubstantiated when the two taxa are studied over their entire North American range (*see* Beringia phase, *S. glauca*).

Salix brachycarpa ssp. *niphoclada* var. *fullertonensis* has been generally incompletely understood because of insufficient collections. However, it was aligned with *S. brachycarpa* by Ball (1948) and with *S. niphoclada* by Raup (1959). Raup chose to reduce it to a variety of *S. niphoclada* on the grounds that its prostrate habit was all that distinguished the two. Although there are other characteristics to distinguish them I have maintained *fullertonensis* as a variety of *niphoclada* and placed them both within *S. brachycarpa.*

A comparison of the infraspecific taxa of *Salix brachycarpa* (Table VI) shows that all are similar in numerous characteristics of taxonomic importance. They can be related by pairs in even more characteristics. As a group they may be distinguished from *S. glauca* by their short pedicels and petioles, and the distinctive oblong leaves with obtuse apices which are borne near the proximal end of vegetative shoots and on the reproductive branchlets. The

TABLE VI. COMPARISON OF THE INFRASPECIFIC TAXA OF SALIX BRACHYCARPA, SSP. BRACHYCARPA (B), SSP. NIPHOCLADA (N), VAR. FULLERTONENSIS (F).

CHARACTERISTICS	TAXA[1]		
	B	N	F
A. Common to all taxa.			
Petiole short, 1-3 mm. long	+	+	+
Ovaries small and short-beaked	+	+	+
Pedicel 0-0.25-0.5 mm. long	+	+	+
Proximal leaves on shoot oblong, apex rounded, obtuse	+	+	+
Bracts sometimes dark-brown to blackish	+	+	+
Anthers small, 0.4-0.5 mm. long	+	+	+
Stomata short, 19.6-20.6 micra long	+	+	f
Petiole reddish	+	f	+
B. Common to ssp. *brachycarpa* and ssp. *niphoclada.*			
Branchlets densely white-villous	f	f	—
Shrub 1-2 feet tall	f	+	—
C. Common to ssp. *niphoclada* and var. *fullertonensis.*			
Aments long and narrowly cylindrical	r	+	+
Shrubs prostrate or decumbent	r	f	+
Leaves generally appressed-pubescent	r	+	+
Leaf apex attenuate-acute	—	f	f
Branchlets thin and flexible	r	+	+
Style short, 0.2-0.5 mm. long	r	+	+
D. Peculiar to ssp. *brachycarpa.*			
Aments small and subspherical	f	—	—
Leaves coarsely pubescent	+	—	—
Bracts greenish in anthesis	f	r	—
Style long, 0.5-0.8 mm. long	f	r	r
Internodes short, leaves appear "fan-like"	f	—	—
Aments crowded on the shoot below the leaves	+	—	—
E. Peculiar to ssp. *niphoclada.*			
Bracts narrow, oblong	r	f	—
Branchlets yellowish	—	f	—
F. Peculiar to ssp. *niphoclada* var. *fullertonensis.*			
Bracts reddish	r	—	f
Branchlets fine appressed-pubescent	r	r	f

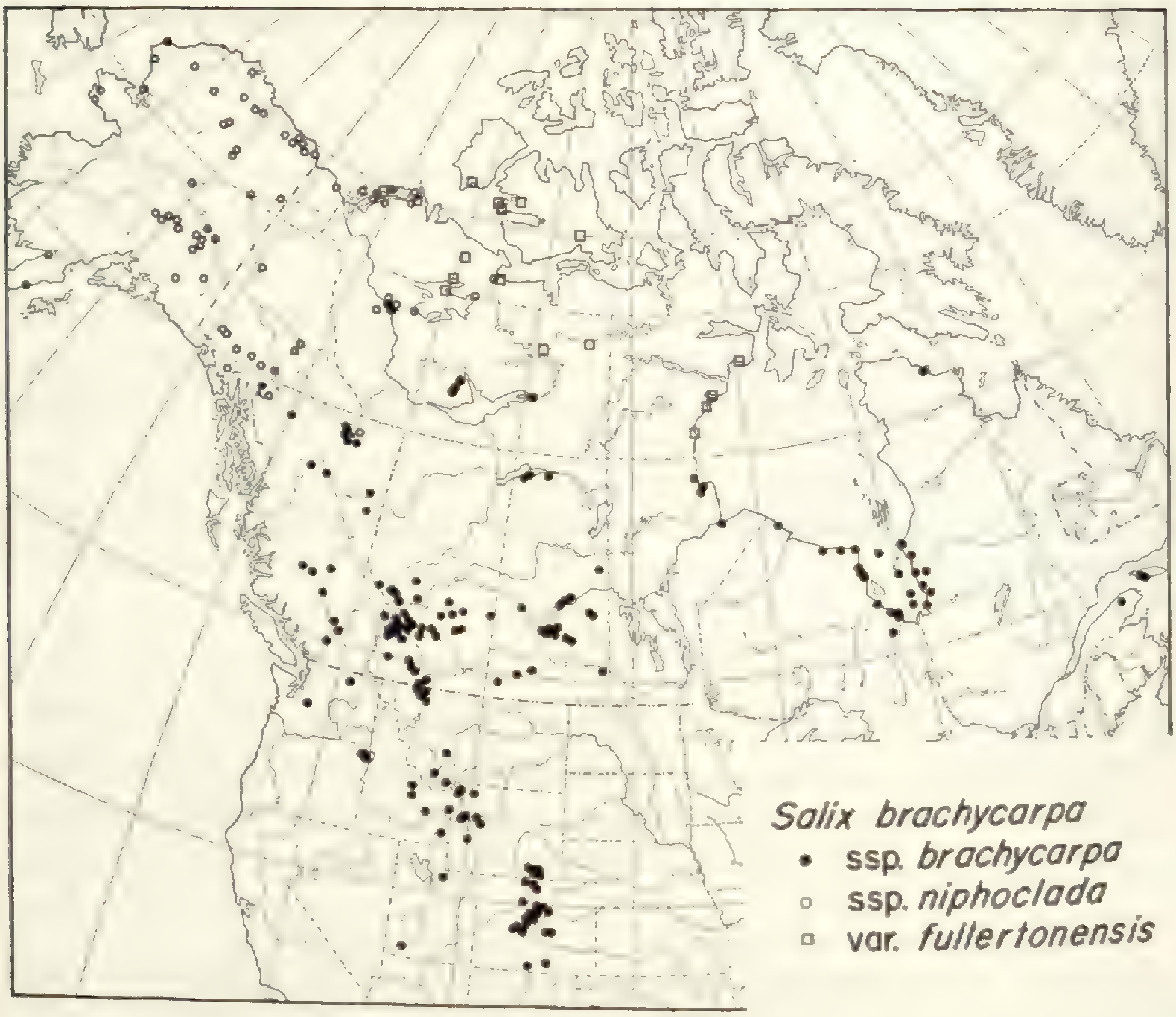
[1]The occurrence of the characteristics is indicated by the following symbols: + = always present, f = frequent, r = rare, and — = absent.

characteristically short anthers (less than 0.5 mm. long) and the short stomata (19.6-20.6 micra long) are possibly related to the diploid condition of *S. brachycarpa* in contrast to the polyploid *S. glauca.*

Salix brachycarpa Nuttall ssp. **brachycarpa.** Figs. 46-50

S. brachycarpa Nuttall, N. Amer. Sylva 1:69. 1842. *Nuttall,* Beer Springs encampment, Bear R., Rocky Mountains, Idaho, 1834. (GH!, type collection).

S. desertorum β stricta Anderson, *in* DC. Prodr. 16(2) :281. 1868. *Bourgeau,* Dans les Marais, Saskatchewan, 16 June 1858. (K, lecto-



MAP 5. Range map of *Salix brachycarpa* ssp. *brachycarpa*, ssp. *niphoclada*, and ssp. *niphoclada* var. *fullertonensis*.

type, A!, fragment and photograph; GH!, syntype ?). *S. stricta* (Anderss.) Rydberg, Bull. N. Y. Bot. Gard. 1:273. 1899.

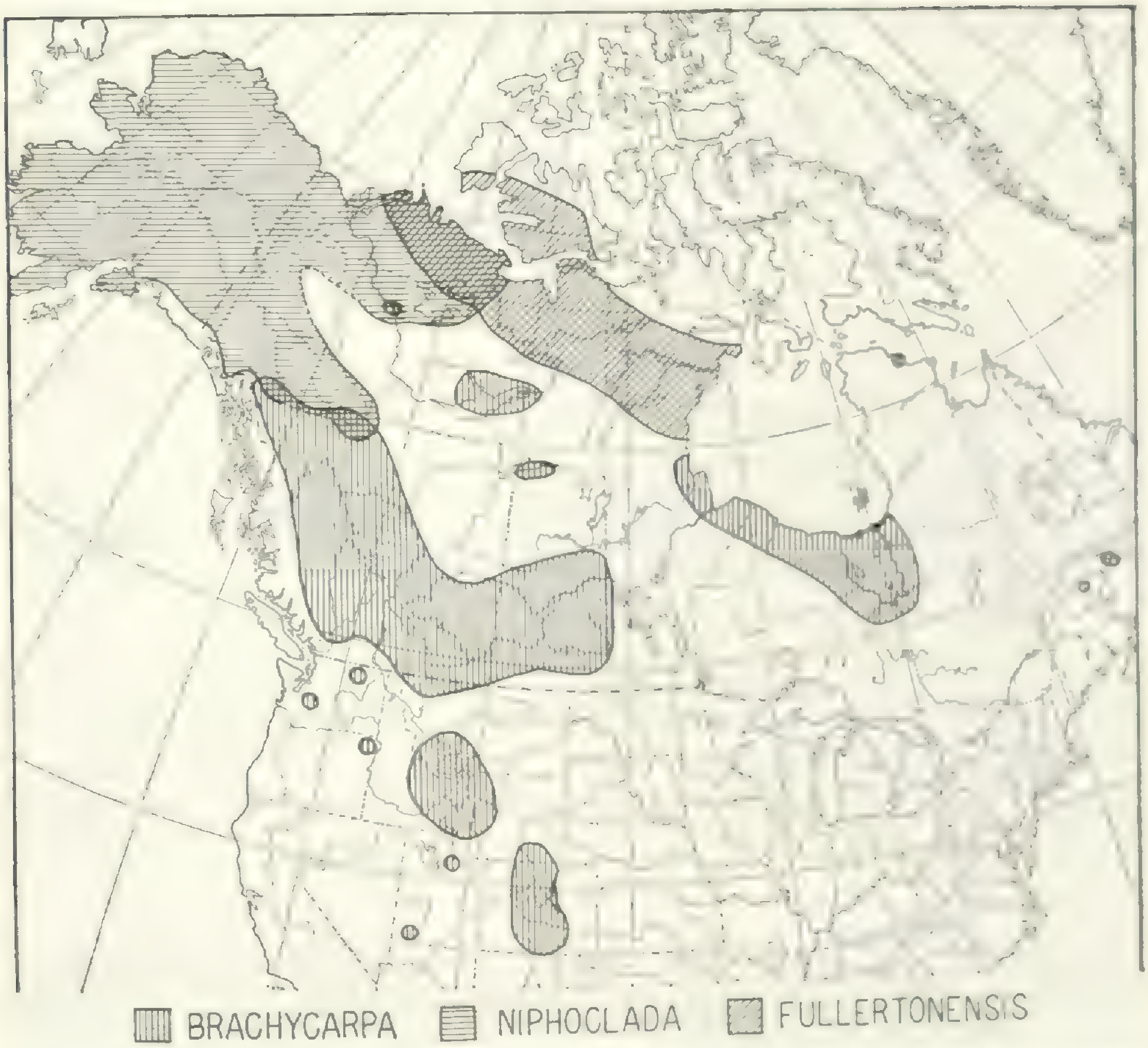
S. desertorum τ *fruticulosa* Andersson, *in* DC Prodr. 16(2):281. 1868. ex char.

S. brachycarpa var. *glabellicarpa* Schneider, Bot. Gaz. 66:338. 1918. *Macoun 95374*, Athabasca R., west side of discharge of Beauvert Lake, Jasper Park, Alberta, 30 July 1917. (CAN, holotype; A!, GH!, NY!, isotypes).

S. brachycarpa var. *sansoni* Ball, Univ. Calif. Pub. Bot. 17:414-416. 1934. *Sanson 119*, Starbird Glacier valley, Rocky Mountains Park, Alberta, July 1928. (RMNP!, isotype).

S. brachycarpa var. *psammophila* Raup, Jour. Arnold Arb. 17:230. 1936. *Raup 6888*, Vicinity of William Pt., Lake Athabasca, Saskatchewan, 16 Aug. 1935. (GH!, holotype; CAN!, GH!, US!, isotypes).

Discussion of Synonymy. *Salix brachycarpa* was collected in Idaho by Thomas Nuttall in 1834 while he was a member of Wyeth's Second Transcontinental Expedition. Authors have incorrectly located the collection locality in Utah, probably because of the reference to Lake Timpangos (now Great Salt Lake) in the original discussion. The collection



MAP 6. Generalized distribution map of the infraspecific taxa of *Salix brachycarpa*. The zones of apparent overlap between the taxa and some probable disjunctions are indicated.

was actually made along the Bear River in the Soda Springs area of southwestern Caribou Co., Idaho. A number of specimens very similar to the type have been collected there. I have not seen the holotype which may be represented by a specimen in the British Museum (P. Raven, personal communication); however, a specimen from the type collection is in the Gray Herbarium.

The names *Salix desertorum β stricta* and *γ fruticulosa* represent *S. brachycarpa*. I have seen a fragment and a photograph of the lectotype of *stricta* which is at Kew, and a specimen in the Gray Herbarium which is probably a syntype. The latter specimen is incorrectly dated 1859; it should read 1858. Both of these specimens are clearly *S. brachycarpa* as was noted by Schneider in 1918 (1918b). The identity of the name *fruticulosa* is less certain because I have not seen any of the type material nor any of the original material studied by Andersson (1868) from Ft. Hall (probably in southeastern Idaho). However, on the basis of its description it can safely be regarded as *S. brachycarpa.*

Salix brachycarpa var. *glabellicarpa* is an unusual form of the species which may be of hybrid origin. It will be discussed below.

Salix brachycarpa var. *sansoni* was described by Ball on the basis of material from the Rocky Mountains of Alberta. I am unable to understand how Ball proposed to distinguish this varietal name from the species. All of the characteristics used to distinguish this name, including the smaller size of the plant, the shorter and relatively broader leaves, and the subsessile, nearly globular aments, are typically those of the species and could not be used to distinguish a variety. The type material *(Sanson 119)* which is supposed to be in the C. R. Ball herbarium (now included in the United States National Arboretum Herbarium) and at the University of California has not been found in either collection. Apparently the only extant specimen of the type collection is an isotype in the Rocky Mountain National Park Herbarium, Banff, Alberta.

The name *Salix brachycarpa* var. *psammophila* is regarded as a pubescent, broad-leaved form of the species which does not require formal recognition. It will be discussed below.

Description. Shrubs erect, commonly 1-3 feet tall, some up to 6-9 feet. Branches reddish-brown, often covered with persistent grayish tomentum, in some cases glabrescent and with a flakey epidermis. Branchlets densely white- or gray-tomentose, some with coarse matted trichomes or only thinly pubescent. Internodes often very short giving the numerous leaves on the shoot a fan-like appearance. Buds reddish-brown, pubescence similar to the branchlets, sometimes pruinose.

Leaves obovate to oval to broadly or narrowly elliptical or rarely oblanceolate, length/width (1.5-) 2.8-3 (-4); length (1.2-) 2.3-3 (-4) cm. long. Apex acute or obtuse depending on the leaf-shape; base commonly rounded. Margin entire, sometimes with a few glands near the leaf-base; veins prominent on mature leaves. Blade pubescent on both surfaces usually with densely matted grayish-white trichomes, sometimes only thinly pubescent; glaucous beneath. Petiole generally shorter than bud (.5-) 1-3 (-4) mm. long; often reddish, sometimes yellowish, the color extending into the midvein. The proximal three or four leaves on a shoot modified from the distal ones, oblong or strap-shaped with a rounded apex and base; glabrous above, long straight trichomes below; sometimes glandular-margined. Stipules present,

FIGS. 46-50. Representative specimens of *Salix brachycarpa* ssp. *brachycarpa*. FIGS. 46 & 47. Staminate specimen, *Argus et al. 90-62A*, 24 June 1962. FIG. 46. General view. FIG. 47. Closeup of staminate aments, note the short reproductive branchlets and the very small anthers. FIGS. 48 & 49. Pistillate specimen, *Argus et al. 90-62B*, as above. FIG. 48. General view, note numerous aments on shoot, each borne on a short, leafy reproductive branchlet. FIG. 49. Closeup of fruiting pistillate aments, note the subglobose shape. FIG. 50. Habit photograph of a low growing specimen from Mt. Albert, Quebec, *Argus 76-59*, 12 July 1959. This specimen was about 20 cm. tall, the hand lens is 5 cm. long. The centimeter scale in the center of the plate is the scale for FIGS. 46 & 48.

usually short (less than 0.5-1.5 mm. long) and broad, often obscured by dense branchlet-pubescence.

Staminate aments coëtaneous, short-cylindrical to often spherical, length × width 6×5, 10×11 or 15×5 mm., borne on very short leafy reproductive shoots rarely over 10 mm. long. Leaves on the reproductive shoot are of the modified type, strap-shaped with rounded apex and base. Aments crowded on the branch, often 14-18 aments on a branch 7-8 cm. long. Bracts light-brown, rarely blackish, often greenish in preanthesis and anthesis; pubescent on both surfaces with straight or curly trichomes; oval to broadly so. Glands borne adaxially and abaxially, usually narrow. Filaments two, free or sometimes united at base, glabrous or sometimes pubescent near base. Anthers small, less than 0.5 mm. long, ellipsoid to globose, yellowish when dry, reddish in preanthesis.

Pistillate aments coëtaneous, short-cylindrical to nearly spherical, length × width 15×10 to 18×10 or 20×9 mm. in postanthesis, borne at the end of short leafy reproductive shoots (peduncle of authors) varying from 3-20 mm. long. Aments commonly very numerous on branches, often 12-15 aments on a branch 13-15 cm. long. Bracts as in the staminate flowers. Ovaries densely white-tomentose, short-beaked. Capsules less pubescent, commonly light-brown, sometimes greenish or reddish. Pedicels characteristically absent or, if present, very short 0.25-0.5 mm. long, pubescent. Glands adaxial, broad or narrow flattened structures, often half as long as ovary. Style mostly entire, about 0.5-0.8 (-1.5) mm. long, sometimes partly divided into two lobes, yellow-green. Stigmas two, each divided into two lobes.

Distribution[1]. (Maps 5 & 6). The distribution of *Salix brachycarpa* ssp. *brachycarpa* is extensive and includes several disjunctions which suggest an even wider distribution in the recent past. The taxon is restricted to North America. Its center of abundance is in the Canadian Rocky Mountains of southern British Columbia and Alberta. From there its abundance diminishes in all directions. It extends southward into Montana, Idaho and northwestern Wyoming, and then into southeastern Wyoming and Colorado. The latter regions are now disjunct but were probably contiguous in the late Pleistocene. West of the center of abundance there are three small disjunct areas in Washington and Oregon. To the north the subspecies ranges into northern British Columbia where it overlaps with ssp.

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[1] A disjunct population of *S. brachycarpa* ssp. *brachycarpa*, on the eastern slope of the Sierra Nevada Mts., California, came to my attention too late to be included in this study. *See* Major, J. & S. A. Bamberg. 1963. Some cordilleran plant species new for the Sierra Nevada of California. Madrono **17**: 93-109.

niphoclada in the region between Muncho Lake and Lake Atlin. The northernmost outlier of this subspecies is at Norman and Norman Wells on the Mackenzie River, N.W.T., where it again overlaps with ssp. *niphoclada*. To the east of the center of abundance it occurs sparsely in the forest-prairie transition of Alberta and Saskatchewan extending northward to the southern shores of Lake Athabasca and to Great Slave Lake. It then occurs in the Hudson Bay lowland region of Manitoba, Ontario, and on the shores of James Bay in Quebec. The gap between Saskatchewan and the Hudson Bay coast is thought to be a real one; however, it may prove to be a collecting gap. In Quebec there are three small disjunct areas, one in northern Ungava at Wakeham Bay, a second on Mt. Albert where the subspecies is isolated on a serpentine plateau, and a third on Anticosti Island in the Gulf of St. Lawrence.

The general pattern of distribution seems to be a large central area in the northern Rocky Mountains with smaller, disjunct areas radiating in all directions. This center cannot be interpreted as a center of distribution because the scattered disjunctions indicate a wide band of "survival" all along the southern fringe of the ice sheet and, in the north, the probable effects of post-Hypsithermal climatic change. The center in the Canadian Rocky Mountains may be regarded as a "center of contraction" rather than a center of distribution.

Discussion. The wide range of *Salix brachycarpa* ssp. *brachycarpa* and its numerous disjunctions are correlated with some morphological diversity, but not enough to undermine the uniqueness of this taxon, one of the most distinctive in the *S. glauca* complex.

In British Columbia and Alberta ssp. *brachycarpa* is relatively constant morphologically but there is some tendency for the species to vary in the direction of *S. glauca*. It must be emphasized that this is only a tendency and that most material is of the "typical" form. This tendency can be noted in certain characteristics including an increase in petiole-length up to 2-3 times the length of the bud, the occurrence of plane leaves correlated with fine appressed pubescence, the occurrence of lanceolate to oblanceolate leaves, and longer beaked capsules. These characteristics occur in much of the material from northern British Columbia and are much less evident in the south. Whether these characteristics are indicative of hybridization and introgression with *S. glauca* is unknown. An artificial cross between *S. glauca (Argus 82S,* pistillate, Churchill, Man.) and *S. brachycarpa* (*Argus 106-59,* staminate, Mt. Albert, Que.) made on 11 April 1960 was successful to the extent that seeds were produced, germinated on 6 June 1960, and the seedlings grew vigorously until killed by a fungus infection in August 1960. It is certainly possible that hybridization may be taking place at present or may have been common at some past time, resulting in the introgression of *S. glauca* characteristics into *S. brachycarpa.*

A modification from the Waterton Lakes area of the Canadian Rocky Mountains deserves comment. This is the glabrous form named var. *glabellicarpa* by Schneider. This variant resembles *S. chlorolepis,* the endemic occurring on Mt. Albert, Que., and the numerous hybrids in that area between *S. brachycarpa* ssp. *brachycarpa* and *S. chlorolepis.* Its most distinctive characteristics are the glabrous-pruinose ovaries and capsules, the generally sparse shoot-pubescence, pruinose stems and buds, longer petioles, and sparsely pubescent leaves. In all of these characteristics it resembles the hybrid *S. brachycarpa* × *chlorolepis.* It resembles *S. brachycarpa* in leaf-shape, pedicel-length, and ament-size and shape. If it were not for the wide disjunction between Mt. Albert and the Canadian Rocky Mountains the specimens of this form would be assigned to the above hybrid. Hybridization may still be the explanation for this form, with *S. pedicellaris* being one of the parents. This is suggested by the long petioles and pruinose caspules. One specimen from the Sunwapta River, Alberta, has patchy pubescence on the ovaries, a characteristic often found in hybrids between species with glabrous and pubescent ovaries. This form requires field study and experimental tests in order to arrive at a more definite conclusion. Investigations could profitably be carried out along the Banff-Jasper Highway in Alberta where this form and the "typical" *S. brachycarpa* occur together.

South of the "center of abundance" there are two large, but isolated, areas of ssp. *brachycarpa.* The northern area, southwestern Montana, eastern Idaho, and northwestern Wyoming, includes the type locality at Soda Springs, Idaho. The subspecies in this region is relatively uniform and individuals with tendencies toward *S. glauca* are virtually unknown. Most of the collections from Idaho are from the salt flats along the Bear River and are more or less identical with the type in having small, elliptic leaves. In this area, leaves on vigorous shoots are broad and have a rounded to subcordate base and rounded apex. This leaf form is found on robust shoots throughout the range of the subspecies. The southern area, southeastern Wyoming, Colorado, and Utah, is characterized by an increasing difficulty in distinguishing ssp. *brachycarpa* from the closely related *S. glauca* and *S. arctica.* In the Medicine Bow Mts. of Wyoming individuals with longer pedicels, blackish bracts, and pruinose stems and buds become increasingly common. I have assumed, in dealing with herbarium specimens, that this form is due to hybridization and environmental modification; however, experimental evidence is much needed. The influence of the environment in the southern Rocky Mts. may be greater than in the north due to the increasing importance of altitude and the sharp environmental changes associated with it. A collection that I have had under cultivation *(C.L. Porter, Aug. 1958)* from the Medicine Bow Mts., Wyoming, has shown such striking leaf and habit modifications that I am reluctant to pass judgment on herbarium material without more personal field experience in this area. The only field studies of environmental modification in *S. brachycarpa* that I know of have been made by Bliss (1956) in the Medicine Bow Mts. Comparisons were made between individuals on north-facing and south-facing slopes. The information obtained in this study is not immediately usable because the identity of the individuals measured is in doubt (voucher specimens *Bliss 419* is identified as *S. brachycarpa* × *glauca*) and the sample size was too small for an adequate comparison of variation.

Southward in Colorado, the problem of recognizing ssp. *brachycarpa* is acute and the distinction between ssp. *brachycarpa* and *S. glauca* is virtually impossible. Specimens with long petioles, yellowish stems and large aments are common, suggesting widespread introgression with *S.*

glauca. The present treatment of the *S. glauca* complex in Colorado leaves much to be desired, and it is obvious that field study is required. Although numerous herbarium specimens are available, they are inadequate for a clear understanding of the problems involved. Other taxonomists, including Ball (1899), Smith (1942), and Schneider (1918b), have come to a similar conclusion.

Along the northern border of British Columbia, from about Muncho Lake to Lake Atlin, ssp. *brachycarpa* is in contact and overlaps ssp. *niphoclada.* Unfortunately, a sufficiently large number of collections of these two taxa has not been made and it is difficult to clearly describe the intergradation that occurs there. Some of the specimens of ssp. *brachycarpa* (*McCabe 8718,* Dease L.; *Setchell & Park 11,* Atlin) suggest ssp. *niphoclada,* the former in pedicel-length and the latter in ament-length; and a specimen of ssp. *niphoclada (Taylor, et al. 250)* shows variation in its vegetative structures in the direction of ssp. *brachycarpa.* The variation found in these few specimens may be found in either subspecies and is not in itself unequivocal evidence of intergradation.

The northernmost extension of ssp. *brachycarpa* is at Norman and Norman Wells, N.W.T., where it appears to be disjunct from the main population. Two specimens from this area *(Crickmay 162* and *A. Porsild 16706)* strongly resemble ssp. *brachycarpa* and two others (*Cody & Gutteridge 7442* and *7656)* are in many respects intermediate between ssp. *brachycarpa* and ssp. *niphoclada.* The Crickmay specimen is a peculiar one with the dense pubescence of the "*psammophila*" type identical to that of *Lainge 222* from Lake Athabasca. From the region between Norman and Lake Athabasca I have seen several collections of ssp. *brachycarpa* from Great Slave Lake *(Thieret & Reich 6838, 7658, 7659, 8268)* and several specimens which seem to represent *S. brachycarpa* × *glauca (Raup & Abbe 4508* and *4597; Loan 312;* and *Cody & Matte 8613).* A possible explanation of the outliers at Norman and Great Slave Lake is that they represent a formerly greater range of the species in the Mackenzie River valley, which has contracted as the region became more stabilized after the retreat of the ice sheet and the drainage of lakes. It is also possible that the gaps are due to inadequate collecting.

There occurs on the south shore of Lake Athabasca a distinctive form of *S. brachycarpa* named var. *psammophila* by Raup (1936). This form is restricted to the sand-dunes. Raup stressed the broadly ovate leaves and the strict upright habit. However, neither of these characteristics is unknown or rare in *S. brachycarpa*. If leaf-length/width is compared in four populations of *S. brachycarpa* ssp. *brachycarpa* (Fig. 51) it is evident that considerable variation and overlap can be observed in this characteristic. The broader leaves in the Lake Athabasca population are part of a continuous variation of this characteristic in the species. The strict upright habit in the sand-dune material seems to be produced by a marked shoot elongation which may be related to the sand dune environment. Low growing, almost prostrate, specimens of *S. brachycarpa* from Mt. Albert, Que. (Fig. 50) assumed an erect habit when grown in the

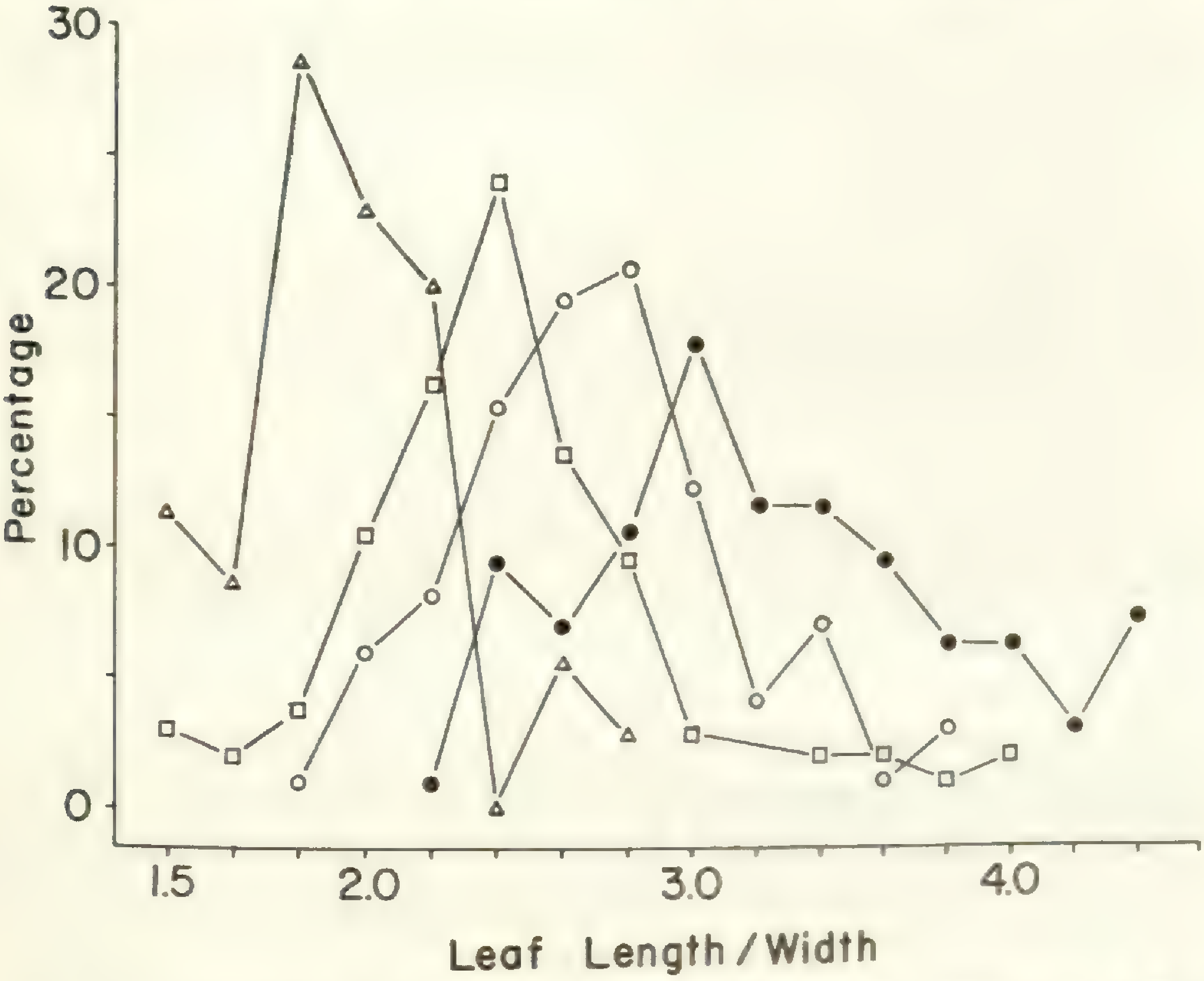

Fig. 51. Comparison of leaf length/width ratio in four local populations of *Salix brachycarpa* ssp. *brachycarpa*. The triangles represent a population from the sand-dunes on the shore of Lake Athabasca (*Argus 448-62*, 8 July 1962). The squares represent a population from the serpentine plateau of Mt. Albert, Quebec (*Argus M IV*, 11 July 1959). The open circles represent a sand-dune population from Churchill, Manitoba (*Argus M III*, 16 Aug. 1958). The closed circles represent a salt-marsh population from Churchill, Manitoba (*Argus M* II, 11 Aug. 1958). All local population samples are in the author's collection.

greenhouse and nursery in Massachusetts (*Argus 104-59* and *106-59*). The reason for the denser pubescence of both leaves and stems in the sand dune material is not completely understood, but it may also be related to environmental influences. It is interesting to note that *S. silicicola* Raup, the densely pubescent relative of *S. alaxensis* Cov., also occurs in the sand dunes on the south shore of Lake Athabasca.

In the Hudson Bay lowlands region ssp. *brachycarpa* is abundant. At Churchill, Manitoba, the subspecies is distinctive, although it is similar to *S. glauca* in leaf-size and shape. A series of characteristics including the short pedicels and petioles, the coarse leaf-pubescence, short internodes, subglobose to short cylindrical aments and the numerous aments per shoot in ssp. *brachycarpa* are sufficient for positive identification. In this area ssp. *brachycarpa* is a late flowering species which serves both as an identifying characteristic and as a possible means of isolation.

On Mt. Albert, Quebec, ssp. *brachycarpa* is very similar to the type-material of *S. brachycarpa* from Idaho. This may be related to the soils which are ultrabasic in both areas, or it may indicate a similar genetic constitution due to past connections. These strong morphological affinities between the Rocky Mountain and eastern elements of *S. brachycarpa* are reminiscent of that which exists between the Rocky Mountain and the Eastern Phases of *S. glauca*. These east-west ties in both species support the hypothesis that the southern portions of both *S. glauca* and *S. brachycarpa* were relatively continuous and made up a gene-pool continuum during a time when the northern portions, the Beringia and Western Phases of *S. glauca* and ssp. *niphoclada* and var. *fullertonensis* of *S. brachycarpa*, were relatively isolated. It is possible that the disjunct nature of the southern populations is of relatively recent origin.

Ecology. *Salix brachycarpa* ssp. *brachycarpa* is one of the few *Salix*, including *S. exigua* Nutt., *S. candida* Fluegge, and *S. chlorolepis* Fern., which can occur in alkaline and/or saline habitats. It occurs on the serpentine barrens of Mt. Albert, the salt-marshes of the Hudson Bay lowlands, the alkaline meadows of Saskatchewan and Colorado, and hydromagnesite swamps and hot springs in British Columbia. In

Idaho it occurs on salt-flats and on the cones of mineral-springs. However, it is not restricted to these habitats and over its range it may be found to occur in a wide variety of habitats from open woodlands, to bogs, muskegs, meadows, stream- and river-banks, alpine slopes, unstable scree slopes, and moraines. It seems to be particularly adapted to an existence in habitats which experience repeated severe disturbances, such as active sand dunes, seasonally flooded banks of streams and the low-lying estuary-zones of rivers.

SELECTED SPECIMENS. **Northwest Territories:** District of Mackenzie: Mackenzie R., between Blackwater R. and Norman, *Crickmay 162* (CAN); Norman, *A. Porsild 16706* (CAN); Great Slave Lake, *Thieret & Reich 6838, 7619, 7657, 7658, 7659, 8268* (F, GWA); Ft. Reliance, *Larsen*, July 1962 (GWA, WIS). District of Keewatin: Seal R., 40 mi. northwest of Churchill, *E.* and *A. Preble 41 (26* before correction) (NA, NY, US). **British Columbia:** Flying U Ranch, Cariboo, shore of Green L., *Eastham 11523, 11525* (NA, UBC); Kinbasket, Big Bend Highway, *Eastham 16008* (DAO, NA, UBC); Summit Lake, *Fyles* (DAO); Anahim L., *Hatter 1* (UBC); Yoho Nat. Park, Yoho R. near Takakhaw Falls, *Hitchcock & Martin 7681* (A, DS); Mt. McLean, near Lillooet, *Macoun 97770* (GH); 2-3 mi. S. of Kinbasket L., *McCabe 6278* (NA); head of Dease L., *McCabe 8718* (NA); Kicking Horse R., near Field, *McCalla 6998* (NA); Emerald L., *Pease 22361* (GH); head of Findlay R., near Thutade L., *E. Preble & Mixter 671* (US); Muncho L., *H. Raup 10855* (A, CAN); Alaska Hwy., Mi. 347, near Liard R., *H. Raup 11011* (A); Peace, 4 mi. above Carbon R., *H. Raup & Abbe 4308* (A, MIN, NY); Atlin, *Setchell & Parks 11* (NA); Liard Hot Springs, *Taylor, Szczawinski, & Bell 337* (DAO, UBC); Elk R., 34 mi. N. of Natal, *Weber 2323* (GH, NA, NY, UBC, US). **Alberta:** Banff Nat. Park: Saskatchewan R., between Mt. Wilson and Mt. Murchison, *Breitung 3208* (NA); Wapta L., *Macoun 68887* (GH, NA, NY); Banff, *Sargent*, 9 Aug. 1897 (A). Waterton Lakes Nat. Park: trail to Crypt L., *Breitung 16992* (NY). Jasper Nat. Park: Athabasca R., *Jack 2579* (A); below Jasper Sta., *2655* (A, NA); Pyramid L., *Macoun 95776* (A, NA, NY), discharge of Beauvert L., *95804* (A, NA, NY); 31 mi. N. of Saskatchewan R. Trading Post on Banff-Jasper Hwy, *Weber 2486, 2487* (GH, NA, NY). Olds, *Brinkman 1978* (US); Nordegg, *Malte & Watson 16865* (GH), Fish L., *116886* (GH); Calgary, *McCalla 4396* (NA). **Washington:** Okanogan Co.: between Tenasket and Republic, *Alter 14* (NA). Kittitas Co.: Beverly Cr., *Thompson 8885* (A, DS, NA, NY), Boulder Cr., *10697, 10698* (A, DS, GH, NA, NY, RM, US). **Oregon:** Wallowa Mts.: mountain sides near the Lake, *Cusick 2298* (MIN, RM, US); Ice L., *Peck 18442* (NA). Wallowa Co.: upper Hurricane Cr., *Peck 22487* (NY). **Idaho:** Teton Co.: Driggs, *Christ 5382* (NA, NY). Caribou Co.: Bear R., north of Soda Springs, *Christ 8977* (NA, NY); Soda Springs, *Davis 825* (DS, NA): Bannock Co.: Soda Springs, *E. & L. Payson 1723* (GH, NY). Custer Co.: Pahsimeroi R., *Wilson 2658, 2658a* (GWA). **Montana:** Beaverhead Co.: Pioneer Mts., near Sheep Cr., *Hitchcock & Muhlick 12886* (DS, GH, NA, NY). Jefferson Co.: Elk Park, *Rose*, 25 July 1932 (NA). Glacier Nat. Park: Cracker L., *Jack 2158* (A), Piegan Pass, *2210* (A, US); trail to Altyn Mt., *McKelvey*, 28 Aug. 1921 (A); Appekunny Cr., *Standley 16906* (US), trail to Piegan Pass, *17457* (US). White R. trail, *Kirkwood 2284* (GH). **Wyoming:** Yellowstone Nat. Park, Lower Geyser Basin, *Rydberg & Bessey 3913* (GH, NY). Teton Co.: Gros Ventre R., *Tweedy 298* (NY). Sublette Co.: Vicinity of Green R. Lakes, *E. & L. Payson 4528* (GH, NA, RM); Union Pass, *A. Nelson 913* (GH, RM), Union Pk., *1072* (RM). Albany Co.: Telephone Mines. *A. Nelson 7869* (NA), Centennial, *8682* (RM). **Utah:** Iron Co.: Cedar Breaks, *Maguire 20169* (NA). Summit Co.: Wasatch Forest, *Haas 86* (NA). **Colorado:** Boulder Co.: Niwot Ridge, 10 mi. NW of Nederland, *Weber 5532* (DAO). Conejos Co.: along Coneuos R., Cumbres Pass and Platoro Rds., *Weber 7850* (MIN). El Paso Co.: Pikes Pk., *Johnston 2788* (NA); Manitou Reservoir, *Christ 619* (NA). Gunnison Co.: Virginia Basin, *Langenheim 376-48*; Mt. Carbon, *Tidestrom 3835* (NA). Huerfano Co.: Sulphur Springs, *Wooton* (A. US). Lake Co.: Leadville, *L. & E. Kelso 4864* (DAO). Larimer Co.: Rocky Mountain Nat. Park, Trail Ridge, *Smith 208* (NA); Estes Park, *Smith 1031A* (NA). Park Co.: N. of Antero Jct., *Weber, Rollins, & Livingston 6603, 6604* (GH). Summit Co.: Breckenridge, *Christ 3003* (NA). Latitude 39°-41° (near South Clear Cr.), *Hall & Harbour 184, 523* (GH); South Park, *Wolf & Rothrock 819* (GH, NY), *829* (GH, US). **Saskatchewan:** Meath Park, 32 mi. NE of Prince Albert, *Boivin & Breitung 6202* (NA); Beverly, *Breitung 5844* (DAO); Saskatoon, *Fraser 1A* (NA), 31 May 1939 (DAO); *Argus & Ledingham 90-62A, 90-62B* (GWA, SASK); Grand Trunk Railway: Bare Hills, *Macoun & Herriot 70292* (NA, NY); Spy Hill, *70294* (GH, NA, NY); Lake Athabasca: McFarlane R., *Laing 222* (NA, US); *Argus 666-62, 667-62, 800-62, 801-62* (GWA, SASK); Ennuyeuse Cr., *H. Raup 6902* (GH, NY); sand dunes east of William R., *Argus 219-62, 220-62, 239-62, 447-62* (GWA, SASK). **Manitoba:** Churchill, numerous collections by *Argus* during 1958 including *319-58, 381-58, 386-58, 409-58, 411-58, 499-58* (DAO, GH, GWA); *Beckett 41 and 42* (DAO); *Macoun 79156* (GH, NY); *Polunin 1864* (GH). **Ontario:** York Factory, *Scoggan 6104* (CAN, MIN); James Bay, Attawapiskat, *Dutilly & Lepage 15604* (GH); Sutton R., *16939* (GH, NA); 20 mi. south of Cape Henrietta Marie, *31310* (NA); Opinaga R., *31577* (DAO, NA). **Islands in James Bay (N.W.T.):** South Twin Is., *Doutt 2284* (NA). **Quebec:** Wakeham Bay, *Dutilly 6001Z*, staminate only, and *6001Y*, (MIN); Loon Portage, *10320A* (NA); Old Factory, *Dutilly & Lepage 12259* (GH); Walrus Pt., *Dutilly, Lepage, & Duman 32821* (DAO, NA); Anticosti Isl.: Jupiter R., *Rousseau 52007* (GH); *Victorin & Germain 24736* (A, GH, US); Southwest Pt., *27764* (A, GH); Mt. Albert: numerous collections by *Argus* including *52-59*, 53-59*, 54-59*, 56-59*, 74-59*, 76-59*, 79-59*, 87-59*, 102-59*, 104-59,* *106-59* (DAO, GH, GWA); *Clausen & Trapido 2875* (MIN); *Collins & Fernald 65** (A, GH, MIN, NY, US); *Fernald & Collins 513*, 513a** (GH); *Fernald, Griscom, Mackenzie, & Smith 25664** (GH, NA, NY, US); *Victorin, Germain, Brunel, & Rousseau 17601* (A, GH, NY, US).

Salix **brachycarpa** ssp. **niphoclada** (Rydb.) Argus comb. nov. Figs. 52-55

S. lingulata Andersson, *in* DC. Prodr. **16**(2):281-282. 1868. *Kastalsky* (as Kostalsky), Alaxa, 1827. (NY!, type collection).

S. niphoclada Rydberg, Bull. N.Y. Bot. Gard. **1**:272-273. 1899. *Taylor 60*, 30 mi. north of Arctic Circle, Mackenzie R., N.W.T., 18 July 1892. (CAN!, holotype; US!, isotype). *S. glauca* ssp. *niphoclada* (Rydb.) Wiggins, *in* Wiggins and Thomas, Flora Alaskan Arctic Slope, AINA Sp. Publ. **4**:144-145. 1962.

S. brachycarpa var. *mexiae* Ball, Univ. Calif. Publ. Bot. **17**:412-414. 1934. *Mexia 2131*, Muldrow Glacier, Mt. McKinley Nat. Pk., Alaska, 23 July 1928. (A!, GH!, MIN!, NY!, US!, lectotype collection). (in part).

S. glauca × *farrae walpolei* Cov. & Ball, of Hultén, Fl. Alaska and Yukon **3**:528-529. 1943. (in part).

S. muriei Hultén, Fl. Alaska and Yukon **3**:531. 1943. *O. Murie*, Salcha Slough, Alaska, 18 June 1922. (A!, holotype [pistillate shoot]; US!, isotype). *S. niphoclada* var. *muriei* (Hultén) Raup, Contr. Gray Herb. **185**:60. 1959.

Discussion of Synonymy. *Salix lingulata* Anderss. I have studied the specimen in the New York Botanical Garden (ex Herb. Fischer) which Schneider regarded as a cotype of this name. It was collected by Kastalsky in Alaska (as Kostalsky in Alaxa). There are only a few fragments in this collection including two almost complete aments, one pistillate and the other staminate. On the basis of this material I would regard the collection as representing *S. brachycarpa* ssp. *niphoclada.* The filaments are pubescent and more or less united at the base, as in *S. glauca*, but the anthers are small, ca. 0.4 mm. long, as typical of ssp. *niphoclada.* The pistillate ament is in anthesis but its small ovaries and short pedicels strongly suggest ssp. *niphoclada.*

Hultén (1943) discusses this name and notes a specimen he has seen at Riksmuseet, Stockholm, collected by Kastalsky at Unalaska. From his account, this appears to be a possible portion of the type-collection and the equivalent of ssp. *niphoclada,* as he suggests (as *S. niphoclada*). Since the two specimens, known to me, collected by Kastalsky and called *S. lingulata* are probably ssp. *niphoclada,* this name is placed as a synonym of that subspecies. However, additional material which is apparently located at Leningrad should be studied before a final judgment is made.

Salix brachycarpa var. *mexiae* Ball. I agree with Raup (1959) that this taxon is indistinguishable from *S. niphoclada* (ssp. *niphoclada*). However, when all the material cited by Ball is taken into account, a number of hybrids were noted, supporting Hultén's (1943) view that the Alaska population included under var. *mexiae* is a hybrid population. The staminate type *(Mexia 2132)* as well as some of the other specimens *(Mexia 2270,* and *Henderson 15045)* are probably the hybrid *S. brachycarpa* ssp. *niphoclada* × *glauca.*

Salix muriei Hultén. Again I agree with the judgment of Prof. Raup (1959) who notes that this name simply represents a glabrescent extreme of ssp. *niphoclada.* The type-material I have seen certainly cannot be distinguished from ssp. *niphoclada* on any basis except its tendency toward glabrescence.

Salix glauca ssp. *niphoclada* (Rydb.) Wiggins. In this combination the taxon ssp. *niphoclada* has been incorrectly associated with *S. glauca.* Wiggins apparently based his judgment on a familiarity with the taxa involved in the Arctic Slope of Alaska region. In this area extensive hybridization seems to be taking place between *S. glauca* and *S. brachycarpa* ssp. *niphoclada* which somewhat breaks down the morphological boundary between these taxa (*see* Hybrids). If these taxa are studied over their entire ranges, the differences between them, which may include cytological differences, and the very close relationship between *S. brachycarpa* and *niphoclada* become apparent.

Description. Low shrubs, erect to prostrate, often spreading, 1-3 (-6) feet tall. Branches thin and flexible, reddish-brown, grayish to yellowish-brown. Epidermis exfoliating; sometimes with persistent pubescence. Branchlets densely white-tomentose, often with intermixed long villous trichomes; sometimes only thinly appressed-pubescent. Buds reddish-brown, with pubescence similar to the branchlets, rarely pruinose.

Leaves obovate, elliptic-oblong, oblong, oblanceolate to lanceolate; length/width (2.1-) 2.9-3.7 (-5.5). Blade (2.1-) 2.5-3.2 (-3.5-4.5) cm. long; apex acute-attenuate; base cuneate to rounded. Margin entire, glandular along the lower margin of the proximal leaves on shoot; veins inconspicuous. Blade pubescent on both surfaces; appressed-tomentose beneath, or sometimes with spreading trichomes, glaucous;

FIGS. 52-55. Representative specimens of *Salix brachycarpa* ssp. *niphoclada*. FIGS. 52 & 53. An erect specimen from the Porcupine River, Alaska. *Buckley* [illegible]. 19 July 1957. FIG. 52. General view, note the narrow leaves with acute-attenuate apices. FIG. 53. Closeup of fruiting pistillate ament. FIGS. 54 & 55. A prostrate specimen from western Arctic Alaska. ***Johnson, et al.* 215**, Ogotoruk Cr. drainage. 28 June 1959. FIG. 54. General view showing prostrate habit, broad leaves and narrowly cylindrical pistillate aments. FIG. 55. Closeup of flowering pistillate ament.

thinly pubescent to glabrate above, sometimes ciliate on margin and glabrescent toward center of blade. The proximal leaves on the shoot characteristically oblong, glabrous above and with long straight trichomes below; apex and base rounded; veins originating near the leaf base running parallel to margin and terminating near apex. Juvenile leaves often sericeous-appressed-pubescent. Petiole relatively short, but longer than bud, 1-3-4 mm. long; reddish to yellowish. Stipules present, sometimes prominent, 2 mm. or less up to 4 mm. long; lanceolate; glandular-margined; pubescent.

Staminate aments coëtaneous, long and narrowly cylindrical, 16-37 mm. long; borne on leafy reproductive shoots (peduncle of authors). In one specimen *(Spetzman 2701)* the flowers are "whorled" on the rachis reminiscent of *S. nigra* or *S. amygdaloides.* Bracts similar to the pistillate aments, but often with short curly pubescence on both surfaces. Glands adaxial and abaxial, narrowly linear, often shorter than in the pistillate flowers. Filaments free, rarely united; glabrous. Anthers small, ca. 0.4-0.5 mm. long, oblong; yellowish when dry.

Pistillate aments coëtaneous, long and narrowly cylindrical 2-3.5-5 cm. long in postanthesis; borne at end of leafy reproductive branchlets. Aments not crowded on shoot as in ssp. *brachycarpa.* Several undeveloped flowers often occur near base of ament. Bracts usually yellowish, but with a tendency to be dark-brown or black; pubescent on both sides with short trichomes, or glabrate abaxially and sometimes pruinose; oval to narrowly oblong. Ovaries densely white-tomentose, short, compact, and short-beaked, occasionally long-beaked. Capsules thinly pubescent, light-brown or sometimes greenish, may be deciduous from rachis at maturity. Pedicels (0-) 0.25-0.5 mm. long, sometimes longer, pubescent. Glands adaxial, usually simple narrow structures, sometimes divided into two lobes; often longer than ovary and up to 2 mm. long; 0.5-1.5-2.0 mm. long. Style 0.2-0.5 mm. long, undivided or divided to the base. Stigmas two, each with two lobes 0.2-0.3 mm. long, rarely longer.

Distribution (Maps 5 & 6). *Salix brachycarpa* ssp. *niphoclada* has a northwest American distribution, found most widely on the Arctic Slope of Alaska and in the Alaska Range. From there it extends into the Mackenzie Delta region and southeast into the Great Bear Lake area. In central Alaska its occurrence is scattered and it is poorly known from western Alaska. It extends east and south into the Yukon and northwestern British Columbia where it overlaps with ssp. *brachycarpa.* In the Coppermine area it overlaps with var. *fullertonensis.*

Discussion. *Salix brachycarpa* ssp. *niphoclada* is a distinctive taxon which can be separated from closely related taxa by its short petiole, densely white-tomentose branchlets, narrowly cylindrical often lax aments, short-beaked ovaries borne on short pedicels. It is distinguished with difficulty from var. *fullertonensis,* but a combination of characteristics including its erect habit, densely tomentose branchlets, larger leaves, and the common occurrence of narrow bracts will usually serve the purpose. For further discussion, see var. *fullertonensis* and Table VI.

The leaves of ssp. *niphoclada* are of two general shapes, broad or narrow. The former are generally elliptic and the latter oblong, oblanceolate or lanceolate. The apex is usually acute-attenuate in both types, although the broad leaves are sometimes more or less obtuse. These two general shapes occur at random throughout the range of the subspecies. Individuals with broad leaves, such as *Raup 12185,* Lake Kluane, Yukon; and *Johnson, et al. 215* (Figs. 54 & 55), Bering Straits area, Alaska, are not only similar in leaf-shape but also in their general prostrate habit, and narrow, elongate, flexible pistillate aments. Individuals with narrow leaves, the most common type, are distributed from the Yukon westward to western Arctic Alaska and include *Porsild & Breitung 9716; A. Porsild 16705; Taylor, et al. 780; Buckley 110* (Figs. 52 & 53); and *Anderson 4707.* Numerous other examples of these types as well as numerous intermediates could be cited.

In central Alaska and the Yukon Plateau, typical material of ssp. *niphoclada* is less common than in the Alaska Range or the Arctic Slope of Alaska. The form found in this region tends to be the glabrescent one named *S. muriei* by Hultén. In addition, many of the specimens seem to represent hybrids. For example, a specimen from the Porcupine River *(Buckley 111)* which is in most respects like ssp. *niphoclada* (glabrescent form) proved to have large epidermal cells and stomata typical of *S. glauca* suggesting a possible influence of the latter species.

The incidence of hybridization of *Salix brachycarpa* ssp. *niphoclada* and *S. glauca* is apparently very high in arctic Alaska and in the Alaska Range. The intergradation noted in herbarium material from that area is thought to reflect a combination of influences of hybridization, introgression, and environmental modification. From what is known about the plasticity of both *S. glauca* and *S. brachycarpa,* it is conceivable that under the influence of a rigorous environment *S. glauca* could approach ssp. *niphoclada*, and on favorable sites ssp. *niphoclada* could resemble *S. glauca*. Our understanding of the effect of the environment on the morphology of these taxa is wholly inadequate. Field observations correlated with experimental transplants could profitably be made on the Arctic Slope region at the Arctic Research Laboratory at Umiat.

Salix brachycarpa ssp. *niphoclada* is treated here with a relatively narrow range of variation. Specimens of presumed hybrid origin are placed under the name *S. brachycarpa* ssp. *niphoclada* × *glauca*. Characteristics given particular attention in delimiting the subspecies are petiole-length, pedicel-length, ament-length and width, and the density of flowering. The pedicel-length is one of the most reliable, but it is best used in combination with other characteristics. In treating this taxon in a fairly narrow sense I have attempted to eliminate many of what appear to be hybrid specimens which have been included in it in the past and which led Hultén (1943) to consider this taxon to be composed largely of hybrids.

The area of overlap between ssp. *niphoclada* and ssp. *brachycarpa* in northern British Columbia has been discussed under the latter subspecies.

Ecology. The ssp. *niphoclada* occurs in a variety of habitats, usually, but not always, in arctic or alpine areas. In the Arctic it occurs on limestone scree, talus slopes, tussock meadows, upland *Dryas* heaths, willow scrub along river and creek banks and on sandy and gravelly floodplains. In the alpine region of Mt. McKinley Nat. Park, it occurs in woods, on moraines, and most commonly on gravel glacial outwash plains.

SELECTED SPECIMENS. **Alaska:** Aleutian Is., "Alaxa" (Unalaska), *Kastalsky* (NY). Western Pacific Coast district: Cold Bay, across from Kenai Pen., *Beals 24* (NA); Koggiung, *Muller 1046* (US); northeast of Naknek Airfield, *K. Raup 11* (US). Bering Straits district: Nome, *Jones 9045* (DS, NA); Kotzebue, *Anderson 4707* (NA); *Scamman 6458* (GH); Grantly Harbor, *Walpole 1752b* (US); Ogotoruk Cr., *Johnson, Viereck, & Melchior 148* (ALA), *215, 215A*, Kukpuk R., *673* (ALA, GWA). Central Yukon district: Gerstle R., *Argus 529, 530* (GWA, RM), *556* (DAO, GWA, RM); Porcupine R., *Buckley 110, 111* (GWA); *Funston 185* (NA, NY, US); Wiseman, *Jordal 1795* (NA, US); Coldfoot, *Piper 270* (NA, US); John R., *Schrader*, 10 July 1901 (US); Anaktuvuk R., *Schrader*, 5 Aug. 1901 (US); Ft. Yukon, *W. & C. Setchell 397* (NA). Alaska Range district: Mt. McKinley Nat. Pk.: Teklanika R., *Argus 608* (GWA, RM); trail to McKinley bar cabin, *658* (GWA, RM); Toklat R., *687* (RM); Savage R., *Mexia 2083, 2084* (A, GH, MIN, NA, NY, US); Thoroughfare R., *Viereck 1097* (GWA); jct. of Glacier Cr. and Thoroughfare R., *1320* (GWA), Jarvis Cr., *Cody & Webster 4999* (DAO); Nabesna Rd., Mi. 91, *Dutilly, Lepage, & O'Neill 21499* (NA); Black Rapids Glacier, *L. & T. Viereck 2139* (GWA); Paxson, *West S.4* (NA). Arctic Coast district: Anaktuvuk Pass, *Spetzman 1766, 2701* (MIN, NA); Umiat, *Churchill 477* (NA); *Lepage 23688* (DAO); *Spetzman 2709* (MIN, NA); Jago R., *Cantlon & Gillis 57-622* (GH); Okpilak R., *57-1844* (GH); Okpilak L., *Cantlon & Malcolm 58-59* (GH); Lake Schrader, *Spetzman 666* (MIN); Canning R., and Ignek Cr., *3881* (MIN); Meade R., *Ward 1193* (DS); Utukok R., *1388* (DS, RM); Icy Reef, *Johansen 160* (NA). **Yukon:** bet. King and Kay Pts., *A. Porsild 7173* (CAN); Dawson, *Eastwood 723* (A); Kluane L., *Anderson 9379* (CAN, NA); *H. Raup 12185, 12404;* Burwash Landing, *13287A 13940, 13961, 13968* (A); Alaska Highway, Mi. 1021, *11819, 11902* (A); Carcross, *Eastwood 722* (A); Mt. Caribou, *Gillett & Mitchell 4527;* Teslin L., *Dutilly 28439* (NA); Canol Rd., Lower Lapie R. crossing, *A. Porsild & Breitung 9716* (CAN, GH, NY, US); Rose Lapie R. Pass, *10056* (GH, NY, US), *10125* (CAN, GH, US). **Northwest Territories:** District of Mackenzie: 6 mi. S. of McKinley Bay, *Cody & Ferguson 10923* (DAO); Schooner Landing, mouth of Anderson R., *10939* (DAO); Ft. Barbant, *Dutilly 18406* (DAO, NA); Mackenzie R. delta, east branch, *A. Porsild 7382* (CAN); Liverpool Bay, Nicholson Is., *A. & R. Porsild 2862* (GH); Coppermine, Cemetary Is., *Findlay 121* (DAO), *122* (DAO, MIN, NY); Great Bear L., east end of McTavish Arm, *Schacklette 3245* (CAN, NA, US); Good Hope, 50 mi. below, *A. Porsild 16739* (CAN, GH); Norman, *16705* (CAN); Norman Wells, *Hicks 1* (DAO); Canol Rd., Mi. 32E, *Cody & Gutteridge 7691* (DAO, NA), *7692* (DAO). **British Columbia:** Lake Atlin, *Eastwood 654* (A, US); Alaska Hwy., Mi. 410, McDonald Cr., *Taylor, Szczawinski, & Bell 250* (staminate and pistillate sheets, DAO, UBC).

Salix brachycarpa ssp. **niphoclada** var. **fullertonensis** (Schneider) **Argus, comb. nov. Figs. 56 & 57**

S. fullertonensis Schneider, Bot. Gaz. **66**:340. 1918. *Macoun 79164*, Fullerton, Hudson Bay, N.W.T., 4 Sept. 1910. (CAN!, lectotype; NY! isotype). *S. niphoclada* var. *fullertonensis* (Schneider) Raup, Contr. Gray Herb. **185**:60. 1959. The holotype is supposed to be located at the Gray Herbarium but it has not been located and I have designated the CAN specimen as the lectotype.

Description. Shrubs prostrate, often mat-forming, rising up to 6 inches. Branches thin, trailing in some, and rooting along their length; reddish-brown, sometimes yellowish, the older darker brown and often grayish. Branchlets shiny, sometimes pruinose, or covered with a fine

FIGS. 56-57. Representative specimen of *Salix brachycarpa* ssp. *niphoclada* var. *fullertonensis*. *Savile & Watts 960*, Chesterfield Inlet, N.W.T., 14 July 1950. FIG. 56. General view, note slender, spreading branches and small leaves and aments. FIG. 57. Closeup of staminate ament, note dark-colored bracts (reddish) and small anthers.

appressed-pubescence, rarely densely tomentose. Buds reddish-brown to yellowish, rounded at apex, pubescent as the branchlets, sometimes pruinose.

Leaves narrowly elliptic to oblanceolate, obovate or oval; length/width 2.7-3.1-4.2; blade (1.2-) 1.7-2.2 (-2.8) cm. long, (0.4-) 0.7-0.8 (-1) cm. wide; apex acute-attenuate on narrow leaves, obtuse on broader leaves; base cuneate to rounded. Margin entire, veins prominent beneath. Blade pubescence of short appressed trichomes on both surfaces, somewhat less above, glaucous beneath; some pubescent on both sides with a mixture of long straggly and short trichomes. Petiole short 1-2 (-3) mm. long; usually reddish, the color sometimes extending into the midvein and around the leaf-margin. Stipules present, 0.3-1-2.5 mm. long, narrow, acute, and glandular-margined.

Staminate aments coëtaneous, narrowly cylindrical, 1-1.5 cm. long, borne on short reproductive shoots. Bracts light-brown to almost black, commonly reddish, puberulent on both surfaces. Glands adaxial and abaxial. Filaments two, free, glabrous, and sometimes pinkish. Anthers 0.2-0.5 mm. long, reddish in anthesis, drying dark or sometimes yellowish.

Pistillate aments coëtaneous, narrowly cylindrical, 1.5-2.5 cm. long, loosely flowered, borne on short reproductive shoot. Bracts as in the staminate flowers. Ovaries densely tomentose, short-beaked. Capsules thinly pubescent and often reddish or light-brown. Pedicels 0-0.3-0.5 mm. long, pubescent. Gland adaxial, narrow and often half as long as ovary; in some several narrow glands are arranged around the ovary. Style entire or minutely divided, 0.2-0.5 mm. long. Stigmas two, divided, short.

Distribution (Maps 5 & 6). This variety is restricted to the western Canadian Arctic, its range not extending south of the tree line. It occurs from the western Canadian Arctic Archipelago, Victoria and Banks Islands, south to the Mackenzie Delta region, and northeastern Great Bear Lake; from there eastward across the Northwest Territories to the west coast of Hudson Bay as far south as Cape Eskimo.

Discussion. *Salix brachycarpa* ssp. *niphoclada* var. *fullertonensis* is an arctic variety in the *S. glauca* complex (Ball, 1948) and clearly related to *S. brachycarpa* (Table VI). It can be distinguished from the other infraspecific taxa in *S. brachycarpa* by its prostrate habit, long trailing branches with appressed pubescence; small leaves with acute attenuate apices; its small, narrowly cylindrical, few-flowered aments; and flowers with reddish bracts, drying blackish (*see* Figs. 56-57). The presence of stomata in the upper epidermis was noted by Schneider (1918b). This observation was verified in the specimens I have examined (Table I); however, its taxonomic importance is not certain. Stomata size also diverges somewhat from the "typical" pattern in *S. brachycarpa* so that two mean stomata lengths have been cited for the variety (Fig. 2); one *brachycarpa*-like with a mean of 20.2 microns and the other *glauca*-like with a mean of 27.8 microns. This evidence suggests that var. *fullertonensis* is not a homogeneous unit, but may include environmentally modified forms of other taxa (e.g. *S. glauca*) or perhaps hybrids.

The type-material of ssp. *fullertonensis* and ssp *niphoclada* is strikingly similar and not easily separated. However, var. *fullertonensis* can be distinguished from the rest of ssp. *niphoclada* by its prostrate habit and characteristically diminutive vegetative and reproductive structures. If it were not for the geographic integrity of var. *fullertonensis* it would be possible to treat it merely as an environmental variant.

The common occurrence of reddish bracts in var. *fullertonensis* and the occasionally pink filaments of the stamens are of interest because a similar feature in *S. brachycarpa* ssp. *brachycarpa* was noted at Churchill, Manitoba. There, the "pinkish" color in the aments occurred at random and was relatively uncommon in the populations, in contrast to the common occurrence of reddish bracts in var. *fullertonensis.*

Herbarium specimens from the Cape Eskimo area of Hudson Bay have a more robust aspect with leaves similar to typical ssp. *niphoclada* and aments resembling those of *S. glauca* (Eastern phase). The taxon in this area is further complicated by the possibility of hybridization between it and *S. arctophila.* Some of the specimens assigned by Schneider (1919) to *S. hudsonensis* Schneid. are very similar to the Cape Eskimo material of var. *fullertonensis.* It should be noted that *S. hudsonensis* was first recognized by Schneider (1918b) as the hybrid *S. fullertonensis* × *groenlandica* (= *S. arctophila* × *brachycarpa* var. *fullertonensis*). On the basis of the material I have available, I cannot formulate an adequate understanding of either *S. hudsonensis* or var. *fullertonensis* in this area, and I prefer not to recognize the above hybrid. Collectors are urged to collect large series of specimens, in various stages of ontogenetic development in this general northwestern Hudson Bay region. For the present, Cape Eskimo material is included in var. *fullertonensis* with some reservation.

E. Hultén (1943) reported *S. fullertonensis* from Nome, Alaska. If it is correct, this would be a considerable westward extension of the range of this western Canadian Arctic taxon. The specimen *(Jones 9045)* on which this report was based is pistillate and differs from var. *fullertonensis* in its large, broad leaves, long stipules, long aments, and stout short stems lacking the flexible trailing character of the variety. In some ways it suggests a depauperate individual of *S. glauca* (as noted also by C. R. Ball). In the present treatment, it is included in ssp. *niphoclada.*

Ecology. *Salix brachycarpa* ssp. *niphoclada* var. *fullertonensis* occurs in the dry rocky tundra where it forms compact mats of vegetation. It is common in highly exposed situations and accordingly modified by the wind. Polunin (1940) reports it chiefly as a plant of the "damper types of heath, and especially in the outermost zones of snowdrift areas." He comments that it has no apparent ecological significance.

SELECTED SPECIMENS. **Northwest Territories:** District of Mackenzie: Muskox L., Back R., *Chillcott 177* (DAO); Toker Pt., *Cody & Ferguson 9851* (DAO); Great Bear L.: north shore of Dease Arm, *A & E. Porsild 4685* (CAN, NA); Cape McDonnel, *5137* (CAN, GH). District of Franklin: Banks Is., DeSalis Bay, *Dutilly 18956* (GH, NA); Victoria Is., Holman Trading Post, *A. Porsild 17270* (CAN, NA). District of Keewatin: Cape Eskimo, *Macoun 79161* (GH, NA, NY); Mistake Bay, *A. Porsild 5652* (GH); Ranken Inlet, *Macoun 79163* (NA, NY), *79165* (NY); Fullerton, *79164* (CAN, NY); Chesterfield Inlet, *Malte 120565* (NA, NY, US); *Savile & Watts 960, 1206, 1207,* and *1459* (DAO, NA).

Map 7. Distribution of hybrids involving members of the *Salix glauca* complex in the Western Hemisphere.

HYBRIDS. MAP. 7

Salix arctica × brachycarpa ssp. brachycarpa. I have seen specimens, which presumably represent this hybrid, from Wyoming and James Bay. However, their identity is somewhat doubtful and the specimens cited are *brachycarpa*-like in most of their characteristics with only glabrous and pruinose stems and buds to suggest *S. arctica.* **Northwest Territories:** James Bay, South Twin Isl., *Baldwin 1623* (GH). **Wyoming:** Albany Co.: Medicine Bow Mts., *Anthony 53* (US); Telephone Mines, *A. Nelson 7926* (NA); Brooklyn Ridge, *J. & M. Reed 2472* (NA).

Salix arctica × glauca. This putative hybrid is characterized by various combinations of the characteristics of *S. arctica* and *S. glauca.* The *S. glauca* characteristics include erect habit, leaves less oblanceolate and without the attenuate base of *S. arctica,* shorter petioles, bracts light-colored with shorter wavy trichomes, and a divided style. The *S. arctica* characteristics include prostrate habit, pruinose stems and buds, sparse branchlet-pubescence, dark-colored bracts with long straight trichomes, leaves with long straight trichomes on the lower surface projecting in a "beard" at the apex, capsules reddish with long stigmas, and dark-colored anthers. The specimens referred to this hybrid combine the characters mentioned in various ways. The pruinose stems and buds seem to be a good indicator of hybridity, especially when correlated with other characteristics. However, some caution must be exercised because this pruinosity is scattered throughout the range of *S. glauca* and there is a possibility that it may indicate hybridization of *S. glauca* and *S. planifolia* as well as *S. glauca* and *S. arctica.*

The occurrence of this hybrid is probably greater than indicated in Map 7. In some areas such as Baffin Island the hybrid has not been recognized because *S. glauca* and *S. arctica* so converge in their morphology that hybrids are impossible to separate from the species.

It was suggested by Schneider (1918b) that *Salix waghornei* Rydb. (Bull. N.Y. Bot. Gard. 1:271-272. 1899. *Bryant,* "Fl. Bor. Am.", 1860) represented the hybrid *S. arctica × glauca.* However, the type material (GH!, isotype) is so fragmentary that I am not able to base a judgment on it.

SELECTED SPECIMENS. **Yukon:** Hearschell Isl., *Dutilly 18281* (NA). Alberta: Jasper Nat. Pk., Mt. Edith Cavell, *Scamman 2440* (GWA), *3187* (GH). **Wyoming:** Medicine Bow Nat. For., Towner L., *Kelso 2201* (GH). **Northwest Territories:** Smith Isl., *Malte 120903* (NY). **Quebec:** Fort Harrison, *Malte 120820* (US); *Wakeham Bay, 120234* (NY); Kogaluk R., *Rousseau 89* (DAO, GH, US). **Newfoundland:** Labrador: Diana Bay, *Dutilly, O'Neill, & Duman 87112* (DAO); Eclipse Harbor, *Potter & Brierly 8602* (NA, US), *8604* (NA); Ekortiarsuk Bay, *Woodworth 169* (A, US). Island Newfoundland: Blomidon Mts., *Fernald & Wiegand 3234, 3235* (GH). Baffin Isl.: Frobisher Bay, Pt. Brewster, *Potter 8671* (NA). **West Greenland:** Disko, Red R., *Grontved 285* (A, US); Umanak, *Floderus 103* (A). **East Greenland:** Blosseville Coast, Manby Pen., *Bartlett 346* (US);

Liverpool Land, *Pedersen*, 15 Aug. 1927 (GH); Skaergaard Pen., *Wager*, 26 June 1936 (DAO).

Salix brachycarpa ssp. **brachycarpa** × **candida.** Specimens of this putative hybrid are known from Anticosti Island, Quebec, and Churchill, Manitoba. The Churchill specimens, recognized in the field as hybrids, were growing on a stabilized beach near Hudson Bay in the vicinity of both *S. brachycarpa* and *S. candida.* I was attracted to the specimens by the unusually dense woolly pubescence on the juvenile leaves, and a characteristic "tufted" pubescence on the older leaves. This, in addition to the small dark-colored bracts, long styles (1-1.5 mm. long) and their general aspect, led me to suspect them to be hybrids. The tufted pubescence, noted on the leaves of the hybrids, is a characteristic of the upper surface of the leaves of *S. candida.*

A similar general morphology characterizes the hybrids from Anticosti Island. These specimens also have aborted ovules which suggests their hybrid nature.

This hybrid was not noted along the floodplain of the Churchill River (Churchill, Manitoba) where *S. brachycarpa* and *S. candida* grow in close proximity. The rarity of the hybrid may be due to the phenological isolation of the species (*see* section on Phenology).

SPECIMEN CITATIONS. **Manitoba:** Churchill, *Argus 475-58, 426-58* (GWA); *Beckett M-17-18* (MIN). **Quebec:** Anticosti Isl., Southwest Pt., *Victorin & Germain 27763* (A, GH, US).

Salix brachycarpa ssp. **brachycarpa** × **chlorolepis.** *S. chlorolepis* var. *antimima* Schneider, Bot. Gaz. **66**:339. 1918. *Fernald & Collins 512c*, Mt. Albert, Quebec, 23 July 1906. (GH!, holotype). *S. brachycarpa* var. *antimima* (Schneid.) Raup, Rhodora **33**:243. 1931, as to name only.

S. × *gaspeensis* Schneider, Jour. Arnold Arb. **3**:80. 1922. *Allen*, 26 July 1881, Mt. Albert, Quebec. (GH!, holotype).

The putative hybrid *S. brachycarpa* ssp. *brachycarpa* × *chlorolepis* only occurs on Mt. Albert where *S. chlorolepis* Fern. is endemic. The hybrid was first mentioned by C. Schneider (1918b) where he noted that Fernald also recognized the hybrid. In 1918, Schneider described *S. chlorolepis* var. *antimima* which, although intermediate, was not thought to be a hybrid because of the presence of stomata in its upper leaf epidermis. However, he did note that some forms were "true" hybrids and in 1922 he described these forms as *S.* × *gaspeensis.*

During a field study in 1959 of the willows occurring on the broad serpentine summit of Mt. Albert, the presence of a hybrid swarm was suspected involving hybridization between the common *Salix brachycarpa* and the relatively rare *S. chlorolepis.* An analysis of the local population on Mt. Albert was made based on field local population samples and herbarium collections. A hybrid index of the type proposed by Anderson (1941) was used. *Salix chlorolepis* can be distinguished from *S. brachycarpa* ssp. *brachycarpa* by its glabrous and pruinose branchlets and buds vs. densely pubescent, non-pruinose branchlets and buds; glabrous leaves, except for a marginal fringe in some, vs. densely pubescent leaves; few-flowered aments vs. many-flowered aments; glabrous and pruinose bracts vs. pubescent, non-pruinose bracts; glabrous ovaries and capsules vs. densely pubescent ovaries and capsules; long, undivided styles vs. shorter, divided styles; and glabrous filaments vs. pubescent filaments. The two characteristics used as "positively identifying" characteristics in the past, bract-color and the presence or absence of stomata in the upper leaf epidermis, were found to be highly equivocal. The green bract color, thought to be distinctive in *S. chlorolepis* (Fernald, 1905, and Schneider 1918b), was shown to be correlated with the ontogenetic stage of development and not restricted to this species. To test the usefulness of the presence or absence of stomata, 30 individuals were examined using the technique described above.

TABLE VII

SPECIES	NUMBER OF SPECIMENS		STOMATA IN UPPER EPIDERMIS
S. brachycarpa	2	—	present
	7	—	present at apex only
	10	—	absent
putative hybrids	3	—	present
	3	—	present at apex only
	1	—	absent
S. chlorolepis	1	—	present
	3	—	present at apex only
	0	—	absent

The results of this survey illustrate the variable nature of this characteristic and it was not used in the hybrid analysis.

Seven characteristics were finally selected to be used in the hybrid analysis and each of 67 individuals in late anthesis or postanthesis was scored for each of them and the scores were totaled. Those with the lowest scores were the most *chlorolepis*-like and those with the highest scores were the most *brachycarpa*-like. The characteristics and their relative scores are given as follows.

CHARACTERISTIC	SCORE		
	0	1	1 or 2
1. Branchlets & buds	pruinose	—	non-pruinose
2 Branchlets	glabrous	thinly pubescent	densely pubescent
3. Buds	glabrous	—	pubescent
4. Leaves	glabrous	thinly pubescent	densely pubescent
5. Bracts	glabrous	—	pubescent
6. Ovaries	glabrous	—	pubescent
7. Style	undivided	partly divided	more than ½ divided

The hybrid population as plotted (Fig. 58) seems to be a relatively accurate representation of the situation prevailing on Mt. Albert. A trimodal curve is produced in which *Salix brachycarpa* and the hybrids are most common and *S. chlorolepis* relatively uncommon. The intermediate taxa described by Schneider, var. *antimima* and × *gaspeensis*, fall into the hybrid zone (between values 2 and 7) and actually outline the hybrid swarm.

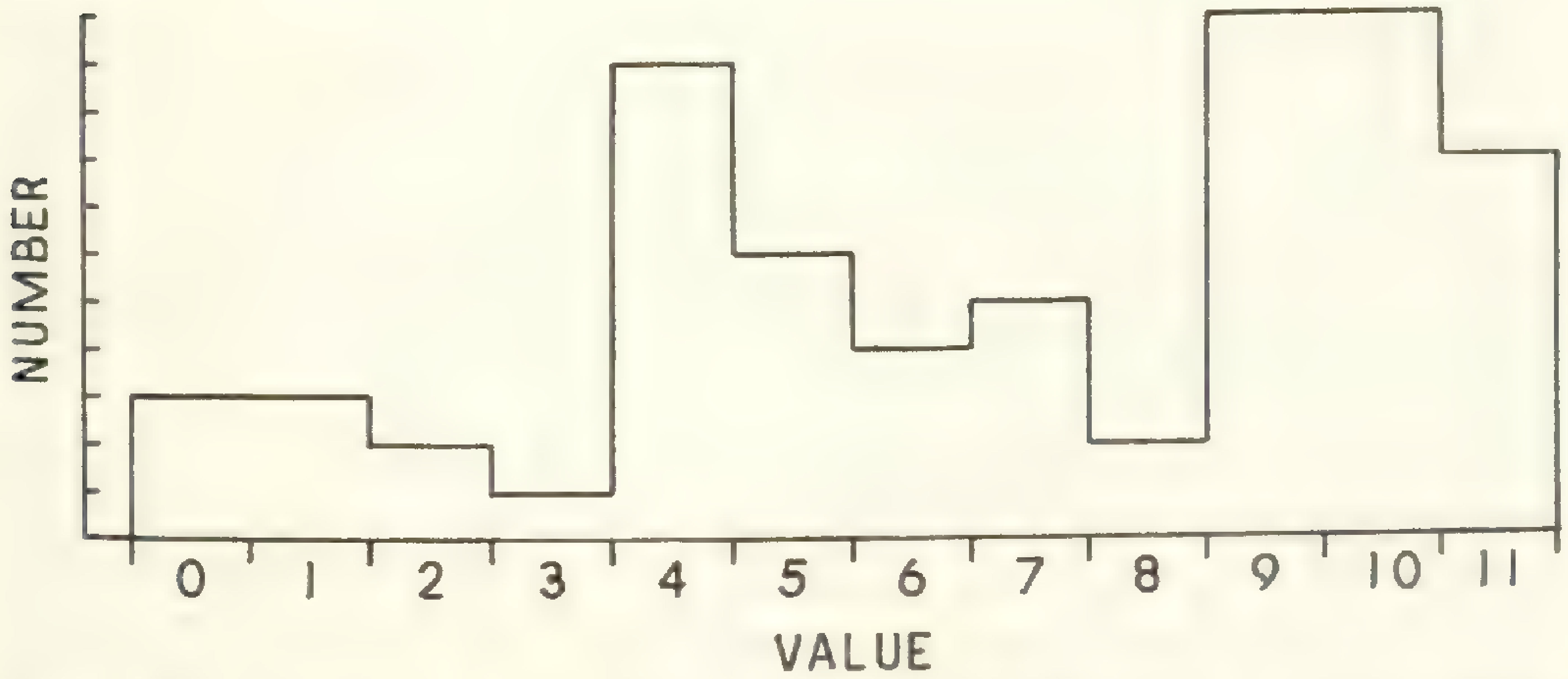

FIG. 58. Histogram of hybrid index values based on specimens of *Salix brachycarpa* ssp. *brachycarpa*, *S. chlorolepis*, and their hybrids from Mt. Albert, Quebec. Typical material of *S. brachycarpa* has values 9-11, typical material of *S. chlorolepis* has values 0-2, and hybrids have values 4-8. The type specimens of *S. chlorolepis* var. *antimima* have values of 2, 3, 4, 5, and 7. The type of *S.* × *gaspeensis* has a value of 5.

Although no one charactisic is sufficient to distinguish the hybrids, a combination of characteristics is more or less definitive. However, problems are often posed by certain individuals, making their identification highly subjective.

On Mt. Albert it is difficult to ascertain whether or not *Salix chlorolepis* is being swamped by hybridization. Since the species is a local endemic its relatively rare occurrence is not surprising and is not in itself an indication of swamping. An experimental cross made between *Salix brachycarpa* (*Argus 106-59*, staminate) and *S. chlorolepis* (*Argus 84-59*, pistillate) resulted in the production of a few seeds, although the ovary was somewhat abnormal. The ovaries of *S. chlorolepis* developed very slowly after fertilization and did not split open at maturity, but remained closed and twisted at the apex. The seeds were removed in the late summer and, although some had begun to dry, they germinated. Three seedlings grew very slowly and died shortly thereafter. Their death is not necessarily a measure of their vitality for the fact that they had begun to dry before removal from the capsule, and the possibility that the growing conditions may not have been ideal, must be considered. However, it does suggest that as a pistillate parent of the hybrid *S. chlorolepis* may not be very effective and that a partial reproductive barrier may prevent a rapid swamping of the rarer species.

SELECTED SPECIMENS. **Quebec:** Mt. Albert, *Allen*, 26 July 1881* (A, GH, MIN, NY); *Argus 63-59*, 65-59*, 70-59*, 78-59*, 83-59*, 96-59, 97-59*, 101-59*, 103-59*, 107-59** (DAO, GH, GWA); *Cerlson*, 31 July 1938* (NA); *Collins & Fernald*, 8-15 Aug. 1905* (GH, NY), *64** (A, GH, MIN, NY); *Fernald and Collins 512a*, 512d*, 512e*, 512, 516, 517*, 519** (GH); *Fernald, Griscom, Mackenzie, & Smith 25667** (GH, MIN, NY), *25668** (A, GH, NA, NY, US); *Gosselin 3624*, 3631** (NA).

Salix brachycarpa ssp. **brachycarpa** × **glauca.** *S. wyomingensis* Rydberg, Bull. Torr. Bot. Club **28**:271. 1901. *Tweedy 3434*, headwaters of Clear Cr. and Crazy Woman R., Big Horn Mts., Wyoming, 20 July - 15 Aug. 1900. (NY, holotype; RM!, US!, paratype). *S. brachycarpa* var. *alticola* Kelso, Rhodora **36**:195-196. 1934. *Kelso 3459*, near Fairplay, Colorado, 10 Aug. 1932. (GH!, isotype).

Hybrids between ssp. *brachycarpa* and *S. glauca* are probably more common than the specimens cited here would indicate. I have been conservative in the recognition of hybrids and the few specimens finally identified as hybrids probably represent only a portion of those present in herbaria. That hybrids can be formed by these species has been partly supported by an experimental cross made in Boston, Massachusetts, in 1960. A pistillate specimen of *S. glauca* from Churchill, Manitoba (*Argus 82S*) and a staminate specimen of *S. brachycarpa* ssp. *brachycarpa* from Mt. Albert, Quebec (*Argus 106-59*) were crossed. Seeds were produced in several capsules and several were germinated and grown into seedlings which ranged in height from 22 to 27 mm. The seedlings grew vigorously for three months until they were killed by a fungus infection. In spite of this evidence few individuals readily identifiable as of hybrid origin were noted in the field (Manitoba or Quebec) or in the herbarium. This may be due to different flowering times, or it may be that hybrid inviability or sterility, not revealed by the single cross made, are important isolating factors. Characteristics, or combinations, indicative of hybridization are not at present well enough known. In the artificial hybridizations made by Nilsson (1930) examples of F_1's which most strongly resembled one parent, and others which looked like a third uninvolved species were noted.

This hybrid has been recognized throughout the area of overlap of the two taxa. Few of the specimens referred to it are intermediates; more commonly they resemble one species or the other but have certain characteristics that suggest hybridity. For example, *Dutilly, et al. 32312*, from Old Factory, Quebec, most closely resembles *S. glauca*, but its densely pubescent leaves and stems, apparently sterile ovaries, and numerous leaves on the shoot suggest hybridization with ssp. *brachycarpa*. Similarly, *Victorin & Germain 24730*, from Anticosti Isl., Quebec, most closely resembles *S. brachycarpa*, but its long aments (ca. 3 mm. long) and its long pedicels (ca. 0.5 mm. long) suggest an influence from *S. glauca*. From the region between Lake Athabasca and Great Slave Lake several specimens resemble *S. glauca* in their general appearance. However, the occurrence of *brachycarpa-*

like pubescence on the leaves of some *(Raup & Abbe 4508, 4597;* and *Loan 312)*, the small ovaries and short pedicels *(Loan 312; Cody & Matte 8613)*, and the reddish petioles on *(Loan 312)* suggest *S. brachycarpa* ssp. *brachycarpa.*

Throughout the southern Rocky Mountains the hybrid seems to be very common. The intergradation which occurs in certain areas between ssp. *brachycarpa* and *S. glauca* suggests that hybridization has been going on for a long time. Specimens from Colorado and Wyoming are often difficult to assign to one or the other species making the identification of putative hybrids highly subjective. Specimens recognized as hybrids have been distinguished by a series of characteristics including pedicels 0.25 mm. long or longer; long cylindrical aments; long beaked capsules, petioles more than three times the length of the buds; and leaves sparsely pubescent. Field study is needed in the southern Rocky Mountains both to understand the parental species and to assess the importance of hybridization between them.

SELECTED SPECIMENS. **Northwest Territories:** Mackenzie R., Mills L. camp, *Cody & Matte 8613* (DAO); Ft. Smith, *Loan 312* (DAO). **Alberta:** Jasper Nat. Pk., Yellowhead Pass, *Jack 2774* (NA); The Palisade, *Jenkins 8002* (DAO); Lake Athabasca, east of Sand Pt., *Raup & Abbe 4508* (GH); north of Sand Pt., *4597* (GH, NA). **Wyoming:** Albany Co.: Centennial, *Jack 1070* (A); Snowy Range, *Bliss 419* (RM); Brooklyn L., *Goodwin & Vestal 801* (GH); Lost L., *A. & R. Nelson 1140* (RM, US). **Colorado:** Clear Cr. Co.: Silver Plume, *Rydberg*, 24 Aug. 1895 (NY); Denver Co.: South Park, Hoosier Pass, *Penland & Hartwell 1310* (NA); Lake Co.: Leadville, *L. & E. Kelso 5128* (DAO); Larimer Co.: Rocky Mt. Nat. Park, Trail Ridge, *Smith 1277* (DAO); Cameron Pass, *270* (NA); Park Co.: Alma, *Ewan 12597* (NA); Antero Res., Buffalo Cr., *Lane 2282* (NA); San Miguel Co.: Ophir, *Maguire* (NA, NY). **Utah:** Kane Co.: Orderville, *B. Maguire 18830* (NA); Utah Co.: Mt. Timpanogos, *Larsen 6798* (US); *Weight 221* (NA); Wasatch Mts., Clayton Pk., *Stokes, 12-26* Aug. 1903 (US). **Manitoba:** Churchill, *Beckett M-17-9* (MIN). **Ontario:** Weenusk, *Dutilly & Lepage 16901* (DAO). **Quebec:** Old Factory, *Dutilly, Lepage & Duman 32312* (DAO, NA); Ft. George, *Dutilly, O'Neill & Duman 97257* (NA); Anticosti Isl., Southwest Pt., *Victorin & Germain 24730* (A, GH).

Salix brachycarpa ssp. **brachycarpa** × **turnorii.** A specimen representing this putative hybrid was collected in the sand dunes on the south shore of Lake Athabasca in 1962. It resembles *S. turnorii* in its red branchlets, prominent, half-cordate stipules, minute glandular teeth on the leaf margin, and pedicels about 1 mm. long; and *S. brachycarpa* ssp. *brachycarpa* in its pubescent capsules, densely pubescent bracts, and densely tomentose immature leaves. Its aborted ovules further suggest its hybrid origin. *Salix turnorii* Raup is endemic to the sand dunes on the south shore of Lake Athabasca and is most closely related to *S. lutea* Nutt. This hybrid is rare in northern Saskatchewan and, although the specimen was growing vigorously, it was apparently sterile and of no evolutionary significance. **Saskat-**

chewan: sand dunes east of William R., Lake Athabaska, *Argus 221-62* (DAO, GH, GWA, SASK).

Salix brachycarpa ssp. **niphoclada** × **glauca.** The specimens identified as this hybrid are not identical with each other in their external morphology, but exhibit various combinations of characteristics suggesting *S. brachycarpa* ssp. *niphoclada* and *S. glauca.* Characteristics indicative of ssp. *niphoclada* are the short petioles, small narrowly elliptic-oblanceolate leaves with acute-attenuate apices, small stipules, and narrow, loosely flowered aments. Characteristics suggesting *S. glauca* are the long petioles, large oblanceolate leaves, large stipules, and densely flowered broadly cylindrical aments.

Specimens that I have studied from the Arctic Slope of Alaska suggest that this hybrid may be more common in that region than indicated by the specimens cited here. Intermediates between ssp. *niphoclada* and *S. glauca* are very common and populations often appear to be hybrid swarms. This situation has led some authors to regard ssp. *niphoclada* as a subspecies of *S. glauca* rather than *S. brachycarpa* as it is treated in the present paper. (Raup, 1959, and Wiggins and Thomas, 1962). This hybrid is also widespread in the Alaska Range area, especially in Mt. McKinley Nat. Park where extensive collections have been made. The staminate type of *S. brachycarpa* var. *mexiae Ball (Mexia 2132, staminate)* referred here to this hybrid also has teratological anthers.

My treatment of this hybrid has been conservative, and I have often placed specimens in one species or the other rather than label doubtful material as a hybrid. Clearly this is the safest course until much more information is available concerning environmental modification, polyploidy, and interspecific hybrid relationships in both parental species.

SELECTED SPECIMENS. **Alaska:** Western Pacific Coast district: Bristol Bay, Kvichak R., *Jones 9257* (DS, NA); Lake Kulik, *K. Raup 415* (US). Central Pacific Coast district: Eklutna Flats, *Dutilly, Lepage, & O'Neill 20081* (NA). Alaska Range: Mt. McKinley Nat. Pk.: *Scamman 5083* (GH); Inspiration Pt., *W & C. Setchell 572* (A, DS, NS, NY, US); Teklanika R., *Argus 605;* Highway Pass, *629* (GWA, RM); Muldrow Glacier, *Mexia 2132,* staminate (A, GH, MIN, NA, NY); Rapids Roadhouse, *W. & C. Setchell 111, 113* (GH, NA); Falls Cr., *Cody 6319* (DAO); Chitna, *Anderson 2021* (NA). Central Yukon R. district: College, *Argus 1089* (GWA); White Mts., *Gjaervoll 859* (CAN); Ft. Yukon, *Henderson 15046* (NA); Fortymile dist., Franklin, *Anderson & Gasser 7212* (GH, NA); Wiseman, *5818* (NA). Arctic Coast district: Pitmagea R., *Shetler & Stone 3256-A* (MICH); Upper Kurupa R. valley, *Hodgdon 8486* (GH); Middle Kurupa R. valley, *8634* (GH, US); tributary west of Chandler R., *Chambers 166* (DS); Sagavanirktok R., *Spetzman 97* (MIN); Okpilak R., *Cantlon & Gillis 57-1937;* Okpilak L., *58-41* (GH). **British Columbia:** Haines Rd., Mi. 60, *Taylor, Szczawinski, & Bell 1177;* Mi. 98, *972* (DAO, UBC). **Yukon:** Dawson, *Eastwood 161* (A, CAN, NA, US); Canol Rd., Mt. Sheldon, *Porsild & Breitung 11610*

(CAN). **Northwest Territories:** Coppermine, *Dutilly 184* (GH).

Salix glauca × padophylla. *S. glauca × pseudomonticola* f. *subpseudomonticola* of Hultén, Fl. Alaska and Yukon 3:529. 1943. *S. princeps-ourayi* Kelso, Biol. Leafl. **34**:11. 1946.

This hybrid was recognized by Hultén (1943) in the Flora of Alaska and Yukon under the name of *S. glauca × pseudomonticola. Salix pseudomonticola* is antedated by *S. padophylla* and the latter name is used in the present treatment (Little, 1953; Argus, 1957). Hultén was of the opinion that this hybrid was very widespread in Alaska and he described three "forms" of it (*see* the synonymy of *S. glauca*). Only his f. *subpseudomonticola* shows definite signs of hybridity, the others represent the "typical" form of the Western phase of *S. glauca.* Specimens identified as this hybrid in the present treatment have glabrate leaves with glandular-toothed margins.

Kelso also recognized this hybrid and named it *S. princeps-ourayi* (1946). The specimen I have seen *(Kelso 5249)* has aborted ovaries, and leaves with toothed margins and rounded bases. It is probably a hybrid but its parentage is not without some doubt.

SPECIMEN CITATIONS. **Yukon:** Dawson, *Eastwood 211* (A, US); Hunker Hill, *Macoun 54399* (GH). **Colorado:** San Juan Co.: Kendall Mt., *L. & E. Kelso 5249* (GH).

Salix glauca × pedicellaris. Much of the material cited as the ferruginous form of the Rocky Mountain phase of *Salix glauca* may, in fact, represent this hybrid. Specimens which strongly suggest a hybrid origin are represented by some of the Thieret and Reich collections from Great Slave Lake *(5416, 5402)*, and by much of the Breitung material from central Saskatchewan *(106, 166, 448, 94, 363, 554, 549, et al.)*. The parents may be *S. glauca* and *S. pedicellaris* but it is possible that similar offspring could be produced by the hybrids *S. glauca × planifolia, S. glauca × scouleriana,* or even *S. pedicellaris × planifolia.*

In some parts of the range of the ferruginous form of *Salix glauca* there is no suggestion of hybridity and many specimens produce seeds which have been germinated (*Argus 517-58, 490-58, 456-58; Breitung 2154;* and *Scoggan 6026, 6088A).* At this time it is impossible to ascertain just how much of the ferruginous form is of hybrid origin, or the exact nature of the hybrid. More study is needed and investigations now underway in Saskatchewan may help answer some perplexing questions. See also, discussion of *S. athabascensis* and *S. fallax* (synonyms of *S. glauca*), and the Rocky Mountain phase of *S. glauca.*

SELECTED SPECIMEN. **Saskatchewan:** McKague, *Breitung 94* (DAO), *106, 166* (A, DAO), *363* (DAO), *448* (A, DAO, NA), *549, 554* (A). **Northwest Territories:** Enterprise-Mackenzie R. Hwy., Mi. 41, *Thieret & Reich 5416;* Mi. 44, *5402* (F, GWA).

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By

Otto T. Solbrig

CHROMOSOME NUMBERS OF CRUCIFERAE

By

Reed C. Rollins

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By
Otto T. Solbrig

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By
Reed C. Rollins

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THE SOUTH AMERICAN SPECIES OF GUTIERREZIA

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Gutierrezia is a small genus of 19 known species in the Compositae-Astereae. Eight species are found in western North America from northern Mexico to southern Canada. The other eleven species grow in South America, from southern Bolivia to the Straits of Magellan. The genus is relatively uniform, particularly in its floral characteristics. Nevertheless, some variability is present in such characters as growth-habit, leaf-size and shape, dimensions of capitula and number of flowers in a head. These fluctuations are most evident among the South American species, where they often can be correlated with the diverse habitats occupied by plants of the genus.

This is the sixth paper in a series dealing with diverse aspects of the evolution and systematics of *Gutierrezia.* The principal objective has been to study the genus from various approaches, such as cytology, morphology, distribution and ecology, including detailed investigations of populations in nature. Previous articles have dealt with generic relationships, variability, cytotaxonomy, and evolution of the North American species (Solbrig 1960a, b, 1964, 1965) and with chromosome morphology (Rüdenberg and Solbrig 1963). The present work covers these aspects for the South American species. A forthcoming work will summarize the evolutionary relationships of the species and the phytogeographical implications of the disjunct distribution of *Gutierrezia.*

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HISTORY OF THE GENUS

The genus *Gutierrezia* with one species, *G. linearifolia*, was described in 1806 by Lagasca. The type material is unknown since no specimens named by Lagasca exist, and the original description is so general that it fits several modern species. Lagasca indicated the original locality only as "Hab. in N. H." (Habitat in Nova Hispania?). The name was subsequently used for at least three different species; *G. resinosa* and *G. mandonii* ssp. *gilliesii* from South America and *G. bracteata* from California.

Hooker and Arnott (1830) described specimens collected in Chile during Beechey's voyage as "*Galinsoga? resinosa.*" Meanwhile Nuttall (1818), unaware of Lagasca's paper, described the new genus *Brachyris*, for the North American species *B. euthamiae* (= *G. sarothrae*). De Candolle (1836) was the first to study the totality of the material then known. He accepted Nuttall's *Brachyris*, with seven species, five from North America, and two from South America: G. *neaeana*, which was based on material gathered by the Malaspina expedition, and *G. paniculata* (= G.

resinosa), which he described without reference to the work of Hooker and Arnott. In addition, De Candolle established the new genus *Odontocarpha,* where he once again redescribed *G. resinosa,* this time as *O. poeppigii.* He placed *Odontocarpha* in the tribe Vernonieae, its clearly asteroid characters notwithstanding.

Hooker and Arnott (1836) recognized that *Gutierrezia* and *Brachyris* were congeneric; Bentham and Hooker (1873) recognized the true identity of *Odontocarpha.* Meanwhile several species from South America had been added to all three genera by Remy, Schulz-Bipontinus, Philippi and Grisebach.

No monographic study of *Gutierrezia* has been attempted since De Candolle. The genus has been treated twice for the flora of Chile: first by Remy (in Gay, 1846) and later by Reiche (1902). With the increase of botanical exploration in South America at the end of the last century, more taxa of *Gutierrezia* were added to the floras of Chile and Argentina by Philippi, Spegazzini, O. Kuntze, Reiche, Cabrera, and Rebeca Acevedo de Vargas. Nevertheless, the areas where *Gutierrezia* grows are not fully explored, and it is likely that new species will be added to the genus in the future.

MORPHOLOGY AND ANATOMY

The importance of a clear understanding of the morphological variation of taxa for taxonomic and evolutionary studies needs no emphasis. Likewise, comprehending the anatomical basis of morphological characters provides illuminating insights for the systematist. Both these approaches have been used in the present investigation. In addition, chromosome number and pollen and stomata size have been investigated whenever feasible.

HABIT: Six of the eight North American species are globose shrubs. This growth-habit also prevails among the austral members of the genus, where it is characteristic of nine of the eleven species. Nevertheless, there is far more variation in these than in the North American species. The other two South American species are appressed cushion-plants or semi-creeping, habits of growth not found elsewhere in the genus. None of the South American species is annual.

Gutierrezia mandonii ssp. *gilliesii* is in habit most similar to the North American species, particularly *G. bracteata* and to populations of large-sized plants of *G. sarothrae.* It is a shrub 40–60 cm. tall, very much branched from the base, with narrow leaves and of globose or semi-globose form. *Gutierrezia mandonii* ssp. *isernii* is similar but less globose, and with more compact branching. *Gutierrezia spathulata, G. ruiz-lealii, G. ameghinoi,* and *G. neaeana* are shorter (10–25 cm. tall), more compact and globose, with wider leaves and with a loose basal rosette of leaves. Similar characters can be observed in *G. mandonii* ssp. *mandonii* of northern Argentina. Of the Chilean species, *G. gayana* is close in habit to *G. mandonii* ssp. *gilliesii*. On the other hand, *G. resinosa* is a large erect shrub with stems up to 5 cm. in diameter, and up to 1.50 m. tall. *Gutierrezia taltalensis* and *G. espinosae* are close to *G. resinosa* in woodiness and other aspects, but they are shorter and more compact in their habits of growth.

Gutierrezia repens is a low, mat-forming or semi-creeping perennial herb, with woody, rhizomatous stems up to 1 mm. in diameter. *Gutierrezia baccharoides* is a true cushion plant that grows in the high Andes above 3,000 m. in Mendoza, and in progressively lower altitudes farther south. It is found at sea-level at the Straits of Magellan.

FOLIAR AND NODE CHARACTERS. Studies of the nodal anatomy of species of *Gutierrezia* always revealed a node with three lacunae and three traces. The traces depart from the stele at different levels, and are normal collateral bundles with exteriorly lying sclerenchymatous fibers (fig. 1).

Foliar anatomy is also very uniform throughout the South American species. To be noted is a very thick cuticle covering an epidermis, formed by large cells, that envelops both foliar surfaces. At regular intervals in the epidermis, there are narrow cavities, where one to several, multicellular, multiseriate resin-glands are found (fig. 10). The resin-glands can also be observed with the naked eye, and are very evident when the leaf is held against the light. They are found on both surfaces but are most abundant in the adaxial surface. Stomata are also to be found on both surfaces but in greater abundance on the abaxial side. The palisade parenchyma is formed of one to three layers depending upon the species, and the spongy parenchyma is normal. The collateral vascular bundles are surrounded by a sheath of collenchyma. The large bundles also include a large resin-canal, and bundle sheath extensions.

Leaf-shape is fairly varied in the different species. Although striking to the eye, the changes involve only variations in length

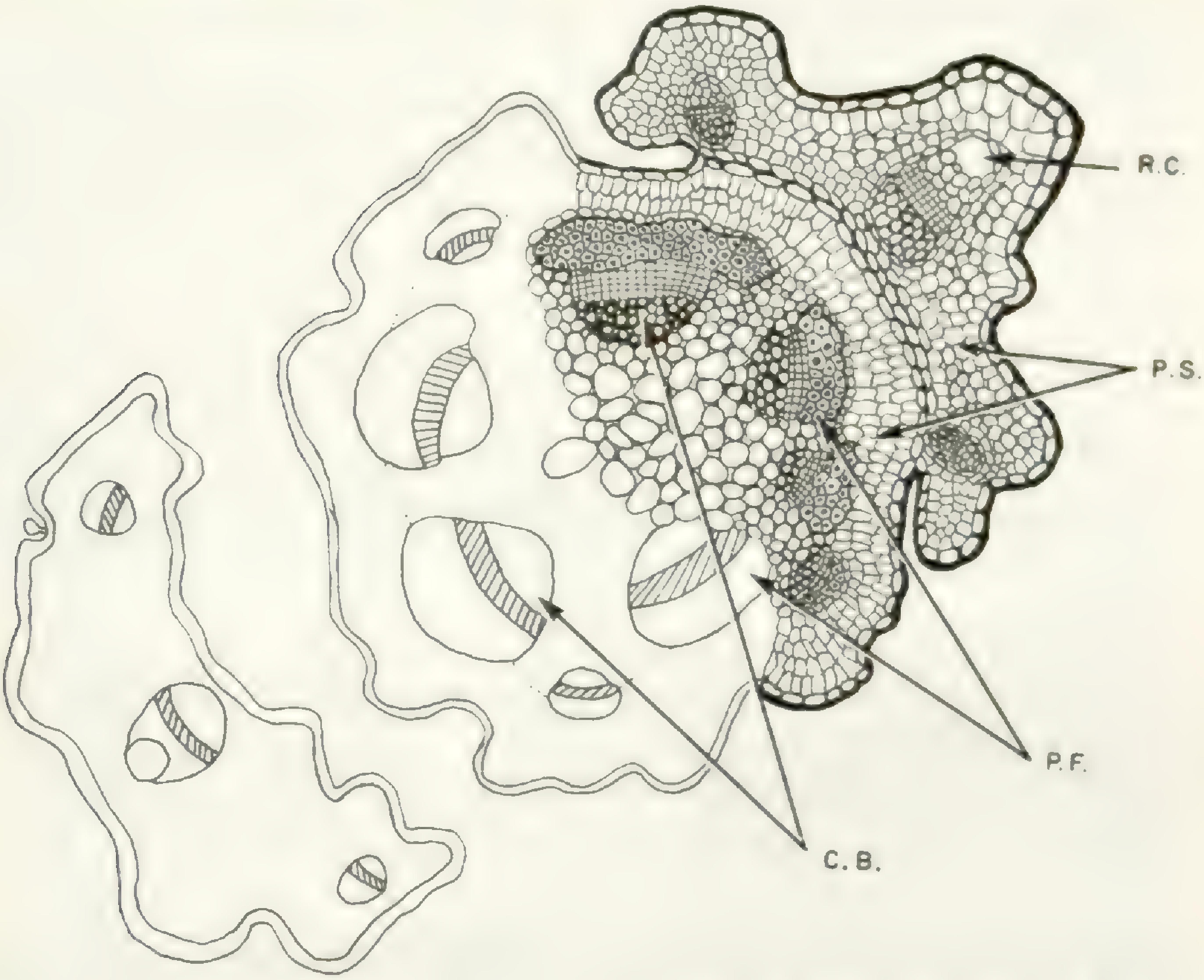

FIG. 1. Camera lucida drawing of cross-section of stem and leaf of *Gutierrezia gayana (Solbrig 3070,* GH), showing some cellular detail, r.c.=resin canal; p.s.=photosynthetic parenchyma; p.f.=phloem fibers; c.b.=collateral bundles.

and width. All species have entire leaves (or minutely toothed under the microscope), linear or lanceolate in shape, with no clearly marked petiole, and with a smooth glutinous surface (figs. 2-18). The changes in shape parallel those in habit, with the more globose species having narrow leaves, that increase in width and decrease in length the more compact and appressed the habit of the species. The extreme condition is reached in *G. baccharoides* where the internodes are very short and the appressed leaves completely cover the stems.

INFLORESCENCE. The capitula are borne on short pedicels in groups of 2-5 in most South American species. In *G. resinosa*, *G. taltalensis*, and *G. espinosae*, the heads are sessile, forming rather tight glomerules, while in *G. repens*, *G. neaeana*, *G. ruiz-lealii*, and *G. baccharoides*, the heads are solitary at the end of the branches.

The capitula in general are small or medium-sized. The only exception is the capitulum of *G. gayana* which is 10-12 mm. in length and up to 15 mm. in width (fig. 22). The next largest

FIG. 2-18. Leaf and involucral bract venation. Veins in black, differences in width due to sclerenchyma. Only major veins drawn. 2. *Gutierrezia espinosae* (*Espinosa, 10-XI-1941*, GH); 3. Leaf of *G. resinosa* (*Solbrig 3044*, GH); 4. Leaf of *G. spathulata* (*Ruiz Leal 9735*, RL); 5. Involucral bract of *G. gayana* (*Solbrig 3070*, GH); 6. Leaf of *G. gayana* (*Solbrig 3070*, GH); 7. Involucral bract of *G. resinosa* (*Solbrig 3044*, GH); 8. Leaf of *G. repens* (*Venturi 4117*, GH); 9. Leaf of *G. taltalensis* (*Johnston 5658*, GH); 10. Resin gland in *G. baccharoides* (*Solbrig 3070*, GH) as seen in cross-section. Similar resin glands are found in the leaves of all species investigated; 11. Leaf cross-section of *G. baccharoides* (*Solbrig 3070*, GH); 12. Leaf of *G. baccharoides* (*Solbrig 3070*, GH); 13. Portion of leaf of *G. baccharoides* with all major and minor veins drawn in; 14. Leaf of *G. mandonii* ssp. *gilliesii* (*Ruiz Leal 21115*, RL); 15. Portion of same leaf of *G. mandonii* ssp. *gilliesii* with major and minor veins drawn in; 16. Cross-section of leaf of *G. mandonii* ssp. *gilliesii*; 17. Leaf of *G. mandonii* ssp. *mandonii* (*Venturi 4853*, GH); 18. Leaf of *G. mandonii* ssp. *isernii* (*Solbrig 3400*, GH).

capitulum is found in *G. repens* and *G. ruiz-lealii* which have heads up to 7 mm. in length and 8 mm. in width, that is, about one half the size of those of *G. gayana* (fig. 20). The smallest heads are those of *G. mandonii,* which are sometimes only 4.5 mm. high and 3 mm. wide. These are only half as large as those of *G. repens* (fig. 21). The other eight species have capitula that range in size between those of *G. mandonii* and those of *G. repens.* The shape of the head varies from species to species, ranging from turbinate to broadly campanulate. The shape is also correlated with the number of flowers: the larger the number of flowers, the more campanulate the capitulum.

In general, the involucral bracts are fairly uniform. However, there are some slight changes from species to species in color, texture, and the degree to which they are appressed. These are of some secondary diagnostic value.

FLOWERS. The flowers of *Gutierrezia* are quite uniform in all the species. There is an outer row of ligulate pistillate flowers, and a number of tubular, hermaphroditic disk flowers. The pappus is formed by 10 to 15 paleae, and the achene is pubescent in all species. The most significant variations are in the color of the flowers, in their absolute size, and in the relative size of their parts.

Gutierrezia gayana is the only species with exclusively white flowers. Six other species have white-flowered populations and/or polymorphic populations. These are: *G. mandonii* ssp. *gilliesii* and *G. ameghinoi,* with a large number of entirely white-flowered populations, and *G. mandonii* ssp. *isernii, G. resinosa, G. taltalensis* and *G. espinosae* with some polymorphic populations containing both white- and yellow-flowered plants. There appears to be no obvious correlation between flower-color and habitat preference other than the fact that all high montane species are yellow-flowered.

Length of the tubular corolla is about 3 to 5 mm., while the tube of the ligulate corolla is a little shorter. The ligule is from 3 to 7 mm. long, and from 1 to 3 mm. wide. Four species, *G. gayana, G. repens, G. ruiz-lealii,* and *G. baccharoides,* have slightly larger flowers and longer ligules than the rest. *Gutierrezia resinosa* has a short and narrow ligule.

The length of the pappus is about 1.5 mm. in the tubular flowers and 1 mm. in the ligulate ones. Exceptions are *G. gayana,*

FIG. 19-23. Flowering heads of *Gutierrezia*. Note the differences in flower number and ligule shape, as well as in size. 19. *Gutierrezia baccharoides* (Pampa de La Poleura, Mendoza, Argentina); 20. *Gutierrezia ruiz-lealii* (Volcan, Jujuy, Argentina); 21. *Gutierrezia mandonii* ssp. *mandonii* (Volcan, Jujuy, Argentina); 22. *Gutierrezia gayana* (Condoriaco, Coquimbo, Chile); 23. *Gutierrezia resinosa* (La Serena, Chile).

where the pappus is usually less than 1 mm. long, and *G. resinosa,* where it is 2.5-3.5 mm. long.

The number of flowers in a head also varies from species to species. The largest number is found in *G. gayana,* where over 50 flowers are present: 15-25 ligulate and 30-40 tubular; *G. repens* and *G. ruiz-lealii* have 10 to 20 ligulate and 17-31 tubular flowers; *G. baccharoides, G. ameghinoi* and *G. neaeana* have more than 20 flowers per capitulum (7-10 ligulate and 10-15 tubular). All the other South American species, with the exception of *G. resinosa,* have 5-10 ligulate flowers and 8-12 tubular flowers; *G. resinosa* has only 4-7 ligulate and 5-12 tubular flowers per head (figs. 19-23).

CHROMOSOME NUMBER AND POLLEN. Unfortunately very little is known about the chromosome number of the South American species of *Gutierrezia.* Altogether only eleven counts have been made (table 1), ten by the author and one by Schnack and Covas. This last count was reported as *Gutierrezia sp.* and no voucher is extant. However, Ing. Agr. Schnack led the author to the exact place where he gathered his cytological material (Papagallos, Prov. Mendoza). The only species growing there and in a radius of 50 miles is *G. mandonii* ssp. *gilliesii.* Since the number of $n=12$ was found in other populations of

TABLE 1. CHROMOSOME NUMBERS OF SOUTH AMERICAN SPECIES OF GUTIERREZIA

Gutierrezia mandonii ssp. mandonii: n=12. Argentina, Jujuy, Maimara, pie del cerro Colorado, *Solbrig 3325;* Argentina, Jujuy, Tilcara, Quebrada del Chorro, *Cabrera & Solbrig 16885;* Argentina, Jujuy, 5 Km. N. of Volcan, *Cabrera & Solbrig 17023;* Argentina, Jujuy, Volcan, Chilcayo, *Cabrera & Solbrig 16838;* Argentina, Catamarca, Tinogasta, Cuesta de Zapata, *Cabrera & Solbrig 16749.*

Gutierrezia mandonii ssp. gilliesii: n=12. Argentina, Mendoza, Papagallos, *Schnack & Covas* (no voucher extant).

Gutierrezia mandonii ssp. gilliesii n=20. Argentina, Cordoba., San Pedro Norte, *Solbrig 3402.*

Gutierrezia ruiz-lealii: n=12. Argentina, Jujuy, cerro Horqueta near Volcan, 3,500 m., *Cabrera & Solbrig 16995.*

Gutierrezia gayana: n=16. Chile, Coquimbo, Cuesta Viñeta near Condoriaco, *Solbrig 3055.*

Gutierrezia resinosa: n=28. Chile, Coquimbo, Rivadavia, *Solbrig 3384;* Chile, Coquimbo, Estancia Huaynay, 45 K. S. of Coquimbo, *Solbrig 3044.*

G. mandonii (but not ssp. *gilliesii*), it appears very likely that Covas and Schnack studied *G. mandonii* ssp. *gilliesii*.

From the available counts it appears that the South American species of *Gutierrezia* are based on x=4 (as are all the North American species studied) and that they are high polyploids. More counts are needed to confirm this hypothesis.

In order to obtain a possible insight into the level of ploidy of the chromosomally unknown species, the diameter of the pollen was measured in 25 samples belonging to nine of the 11 species. Few size-differences were found and in general the pollen-diameter did not correlate with known differences in chromosome ploidy levels. Consequently, pollen-diameter is not a reliable indicator of ploidy level in this group of species.

DISTRIBUTION AND ECOLOGY

Gutierrezia mandonii is the most widely distributed of all South American species of the genus. It is found throughout the region extending from southern Bolivia (Depts. Tarija and Potosí) along the eastern foot-hills of the Andes and the Pampean formation to Mendoza and Córdoba. It also grows in the Sierra de la Ventana in the province of Buenos Aires, and sporadically in south-central La Pampa, and in the southernmost part of the province of Buenos Aires (fig. 24). *Gutierrezia repens* is endemic to the Aconquija Mts. in prov. Tucumán, Argentina, and adjacent areas of Catamarca and Salta, and is found between 2,800 m. and 4,000 m. (fig. 25); *G. ruiz-lealii* is also found at altitudes over 3,000 m. in the mts. of Jujuy and Salta (fig. 26). *Gutierrezia ameghinoi* grows in eastern and northern Patagonia, western Rio Negro, Neuquén, and southern Mendoza in Argentina, at elevations ranging from sea level to 2,000 m. (fig. 25); *G. spathulata* is found on the western slopes of the Andes of southern and central Mendoza between 1,500 and 3,500 m. (fig. 27). *Gutierrezia baccharoides* is a species of alpine to subantarctic environments. It grows from the high Cordillera of Mendoza, where it is found at altitudes ranging from 3,000 to 4,000 m., to the Straits of Magellan, where it grows at sea level (fig. 24). Finally, five species are found in Chile: *G. resinosa*, in the dry mediterranean belt between Santiago and Copiapó at low elevations (fig. 25); *G. gayana* in the dry, pre-Cordilleran "pampas," north and east of Serena (fig. 26); *G. taltalensis* and *G. espinosae* that grow in the extreme desert area of northern Chile, the former in the vicinity of Taltal, the second extending from Taltal to Antofagasta (figs. 24, 27); and *G. neaeana* known only from the type collection (locality unknown) and from one other collection from the high Cordillera of central Chile (fig. 27).

Considering the entire area, the various species of *Gutierrezia* grow in diverse environmental conditions. Unfortunately, problems of transportation and distance made impossible detailed analysis of soils and other ecological factors, as were made for the North American species. Nevertheless, field-observations and data taken from the literature allow a preliminary evaluation of the ecological situation.

SOIL. Analysis of 19 soil samples supporting growth of North American species (Solbrig, 1960a) failed to reveal any differences in edaphic requirements between the species, but provided some indication of the over-all requirements of the genus as a whole. The North American species of *Gutierrezia* seem to grow on loose, sandy, alkaline or neutral soils, and apparently those with also a low content of organic matter and nitrates. Field-observations tend to confirm this set of conditions for the South American species also, at least for seven of the eleven species, which are the ones studied in the field. In addition many of the South American species are found growing among rocks in mountainous areas, and in at least one instance plants were seen growing in scree on a rather steep slope. No South American species grows in a special edaphic situation, such as is the case with the North American species that grow on serpentine. Nevertheless, in certain cases (*Gutierrezia mandonii* ssp. *gilliesii* in Córdoba) *Gutierrezia* appears to grow on limestone outcrops.

BLOOMING PERIOD. Species of *Gutierrezia* bloom principally in late summer and fall. All North American species of the genus show this blooming regime. Rainfall affects blooming time to a certain extent, even within a species (Solbrig, 1964). Observations in the greenhouse, where water was always plentiful, indicate that blooming is a photoperiodic response in the North American species, since under cultivation they also bloomed in late summer and fall. Of the eleven South American species, only one, *G. ruiz-lealii,* appears to bloom exclusively in late summer and fall. However, this might be only an artifact resulting from the very few observations available on this taxon. Four species, *G. repens*, *G. spathulata*, *G. baccharoides* and *G. man-*

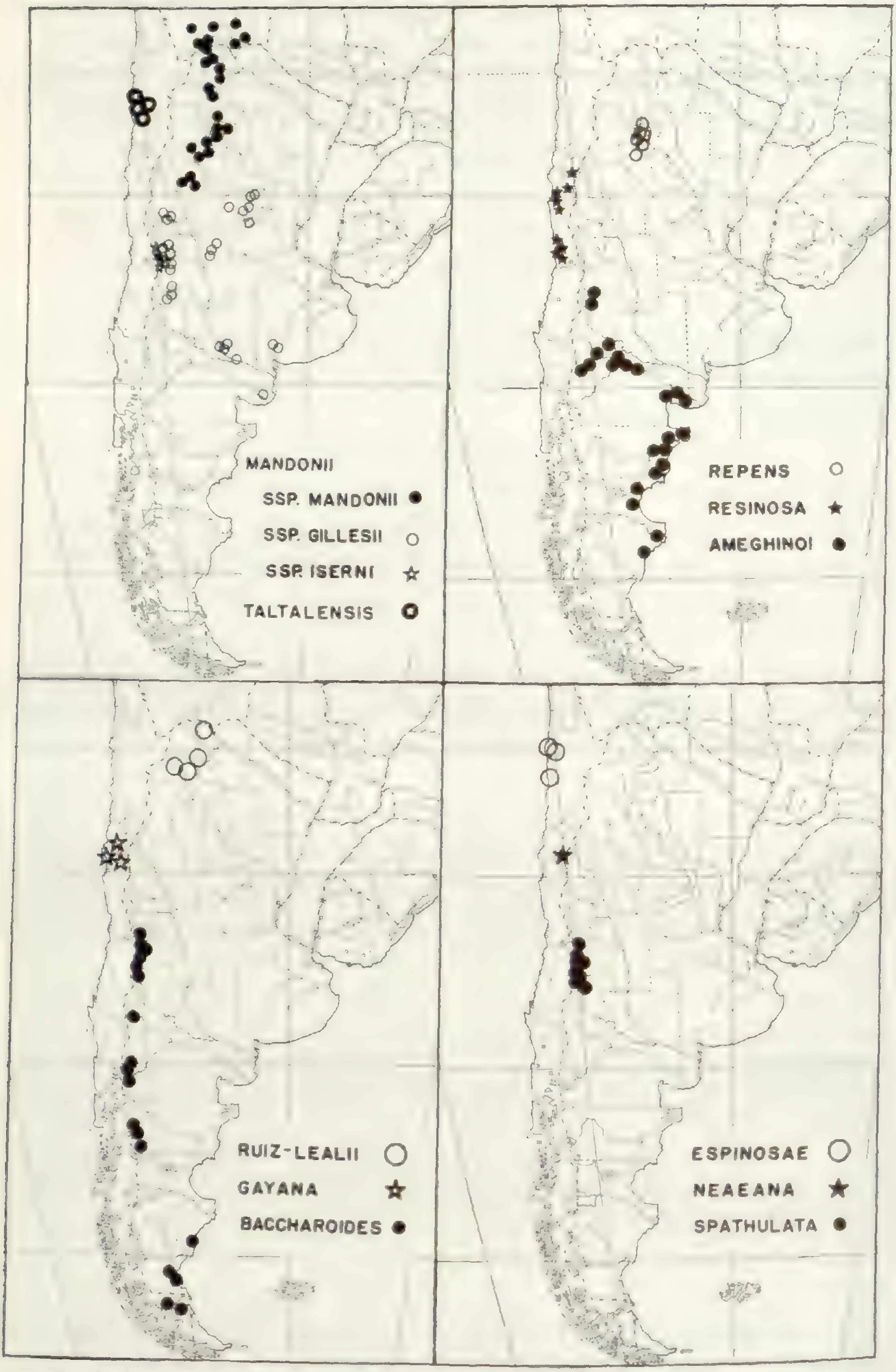

FIG. 24-27. Distribution of the South American species of *Gutierrezia*. Each dot represents a locality; several collections might be known from each locality. Goode Base Map, Copyrighted by University of Chicago.

donii, bloom throughout the summer and early fall, approximately from November-December to May. These species grow in areas with summer rains. Populations of *G. mandonii* ssp. *gilliesii* from Córdoba, an area that has summer droughts, usually bloom later, from March to July. On the other hand, the four Chilean species and *G. ameghinoi,* from Argentine Patagonia, bloom in late spring and early summer, roughly from October to February. This is, no doubt, an adaption to the spring rains of the region where these species grow. *Gutierrezia gayana* is the earliest bloomer of the whole genus, flowering only from September to November. Field-observations further show that sufficient rainfall is needed before blooming will begin in any of the South American species. In very dry years, when rainfall is insufficient, the plants will not bloom at all. Therefore, it appears that in some of the South American species, blooming is controlled by moisture and not photoperiod.

OTHER OBSERVATIONS. North American species of *Gutierrezia* spread into range lands when these are overgrazed. This is apparently due to a disruption of the dynamic balance between grasses and *Gutierrezia* in the competition for water and nutrient matter in the soil. Normally the grasses are able to crowd *Gutierrezia* out from the better soils, the reverse being true in the poorer ones (Solbrig, 1960a). When land areas are overgrazed, *Gutierrezia* can move into the edaphically better places. A similar situation holds true for at least two South American species, *G. resinosa* and *G. mandonii* ssp. *gilliesii.* This is most notable in the region south of Serena, Chile, where extensive overgrazing in open ranges, particularly by goats, has led to a depauperization of the grassland vegetation and the spread of *G. resinosa* over hundreds of acres (figs. 28-30). Fenced, well managed pastures were devoid of *Gutierrezia* plants. The plants are not palatable to cattle, sheep, or goats on account of their high resin-content. There are unconfirmed reports that the plant when ingested in large amounts is poisonous.

The North American species form dense populations of 50 to 1,000 plants. These populations are often separated from each other by considerable distances. This type of distribution is also found in most of the South American species, notably *G. mandonii* ssp. *gilliesii* and *G. resinosa.* On the other hand, the mountain species are less likely to form large populations, and this is particularly true for the two species from northern Chile, *G.*

FIG. 28-30. Natural populations of *Gutierrezia*. 28. Natural population of *G. gayana* at Condoriaco, Coquimbo, Chile. The species is distributed locally over several acres, but the plants are fairly separated from each other; 29. Roadside population of *G. mandonii* ssp. *gilliesii*, near Los Cocos, Cordoba, Argentina. In this area *G. mandonii*

espinosae and *G. taltalensis*. These two species are found in the "quebradas" along the extremely dry coast between Taltal and Antofagasta. Rainfall in this region is, on the average, only 1 mm. per year with many years when absolutely no rainfall occurs. Plants obtain needed moisture from fog condensation in these steep, sea-facing canyons. As a result, the vegetation is very sparse. Bushes of *Gutierrezia* are very rare, often only one in a locality.

BREEDING SYSTEMS AND POLLINATORS. The North American perennial species are self-compatible, but normally outbreeding. This is due to the long exserted styles that make selfing mechanically improbable. The annual species on the other hand have shorter styles and are normally self-pollinated. Unfortunately, no systematic study of the South American species could be made because most species could not be brought into cultivation. The two species that were grown, *G. resinosa* and *G. mandonii* ssp. *gilliesii*, were self-compatible. However, as is the case with the North American species, they were not normally selfed on account of the long exserted styles. Field-observations and herbarium studies show a similar exsertion of the style in all the South American species. It is possible that they all might be self-compatible, but in all probability they are normally outbreeding.

Species of *Gutierrezia* are pollinated by a variety of different insects, particularly small hymenoptera, diptera, and coleoptera. This is true both for the North American species (Solbrig 1960a, 1964) and for those of South America.

Systematic Treatment

Gutierrezia is both a polymorphic and polytypic genus. Consequently the precise delimitation of allopatric taxa is difficult, particularly when there is a lack of biosystematic information. The phenotypic plasticity of the plants complicates matters further. The criteria adopted in the delimitation of taxa are what is usually labelled as "conservative." An effort has been made to delimit natural groups stressing similarities within the taxon rather than differences. Even so, in some cases, certain herbarium specimens—especially incomplete and scrappy ones—do not fall easily in the groups recognized. Future field and experimental work are needed to resolve these problems.

Another difficulty is the imprecise floristic knowledge of many

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forms dense stands, that occupy at most a few hundred square feet at each locality. 30. Population of *G. resinosa* south of Serena, Chile. Due to overgrazing of forage plants, *G. resinosa* has spread over hundred of acres forming rather dense stands.

of the areas sustaining *Gutierrezia*, especially certain areas of Chile. From experience, we know that only in time will the needed collections be assembled.

Gutierrezia Lag., Nov. Gen. et Spec. 30. 1816

Brachyris Nutt., Gen. **2:** 163. 1818.
Brachyachyris Spreng., Syst. **3:** 574. 1825.
Hemiachyris DC., Prodr. **5:** 313. 1836.
Odontocarpha DC., Prodr. **5:** 71. 1836.

Suffruticose, erect, creeping or cushion-forming, glabrous, perennial shrubs. Leaves petiolate or sessile, alternate, subcoriaceous, linear-lanceolate to lanceolate, entire. Heads in corymbose or paniculate inflorescences, in clusters, or solitary at the ends of branchlets. Capitula turbinate or campanulate, the involucral bracts in two to many rows, imbricated. Flowers yellow or white, the ray flowers pistillate, ligulate, the disk flowers tubular, hermaphroditic; corolla with a very short tube and narrow throat, five-lobed; stamens 5; styles of tubular flowers with long branches very much exserted at maturity, long stigmatic hairs present on the upper part and stigmatic papillae on the lower part of the stigmatic branches; styles of the ligulate flowers only papillate; pappus of short to medium-long squamellae, shorter in the ligulate flowers; achenes turbinate, slightly flattened, tomentose, with hairs arranged in loose rows.

Type species, *Gutierrezia linearifolia* Lag. (No specimens identified by Lagasca have been found).

KEY TO THE SECTIONS

A. Plants perennial (shrubs).
  B. Involucre more than 10 mm. in height and width. Flowers white. Plants from South America. section *Megalocephala*.
  B. Involucre less than 8 mm. in height and width. Flowers mostly yellow, rarely white. Plants from North and South America. section *Gutierrezia*.
A. Plants annual. Flowers always yellow. Plants from North America. section *Hemiachyris*.

KEY TO THE SPECIES

A. Cushion or mat-forming, or low creeping perennials, less than 10 cm. tall.

B. Small, compact, cushion or mat-forming plants. Leaves lanceolate, 10 mm. long or less .... 6. *G. baccharoides.*

B. Low, creeping, rhizomatous plants. Leaves 30 mm. or longer .... 2. *G. repens.*

A. Erect to globose shrubs, more than 10 cm. tall (generally 20-80 cm. tall).

C. Involucres more than 10 mm. in height and width; flowers white .... 11. *G. gayana.*

C. Involucres less than 8 mm. in height and width; flowers yellow or white.

D. Involucres narrowly turbinate 6–8 mm. in height, 3–5 mm. in width; erect shrubs with woody bases (plants of Chile).

E. Ligules 1.5 mm. long or shorter; leaves narrow, 1.5 mm. wide or narrower; narrow, open shrubs, 50–150 cm. tall .... 8. *G. resinosa.*

E. Ligule 2.5–3.5 mm. long; leaves broader, particularly the basal ones, 2 mm. wide or more; compact shrubs 25–75 cm. tall.

F. Leaves linear, more than 50 mm. long; stems smooth .... 9. *G. taltalensis.*

F. Leaves lanceolate, less than 45 mm. long (usually less than 15 mm.); stems with prominent elevated leaf scars .... 10. *G. espinosae.*

D. Involucres turbinate, 4–6 mm. high, or campanulate and then up 7 mm. high (Plants of Argentina and Bolivia.)

G. Leaves linear, 2 mm. wide or less; involucres turbinate, 2–4.5 mm. wide .... 1. *G. mandonii.*

H. Plants 50–100 cm. tall; leaves narrow, 1 mm. wide; flowers white or occasionally yellow . 1b. *G. mandonii* ssp. *gilliesii.*

H. Plants less than 50 cm. tall; leaves 1–2 mm. wide; flowers yellow.

I. Leaves short, mostly scale-like, 20 mm. long or less; involucre less than 4 mm. in height .... 1a. *G. mandonii* ssp. *mandonii.*

I. Leaves longer, not scale-like, the longer ones over 35 mm. long; involucre 4–6 mm. high .. 1c. *G. mandonii* ssp. *isernii.*

G. Leaves lanceolate, oblanceolate, or spathulate (at least the basal ones), 3 mm. wide or more; involucres campanulate, 4–6 mm. wide.

J. Leaves oblanceolate; capitula solitary at the end of naked or sparsely leafed scape-like branches, 3–10 cm. long .... 7. *G. neaeana.*

J. Leaves acute; lanceolate or spathulate; capitula in groups of 2–5, or solitary at the end of leafy branches.

K. Involucre campanulate, as wide as high, 5 mm. or more in width; ligulate flowers 8–10; tubular flowers 10–15.

L. Ligules 5 mm. long or more, yellow; involucre 7–10 mm. broad .... 3. *G. ruiz-lealii.*

L. Ligules 3 mm. or less in length, white (or yellow); involucre 5–7 mm. wide .... 4. *G. ameghinoi.*

K. Involucre turbinate, higher than broad, 4 mm. or less in width; ligulate flowers 5–7; tubular flowers 8–12 .... 5. *G. spathulata.*

SECTION GUTIERREZIA

1. **Gutierrezia mandonii** (Sch. Bip.) Solbrig, comb. nov.
Brachyris mandonii Sch. Bip., Linnaea **34:** 354. 1865.

Small to medium-sized shrub, 25-100 cm. tall, from a strong, usually fascicled, root. Caudex strong, woody, up to 2 cm. in diameter, with a thick, usually dark bark, profusely branching to the top. Branches erect, angular, leafy to the end, light gray or green in color, up to 50 cm. long. Leaves linear, with an acute apex, sessile, often somewhat attenuate towards the base, 5-30 mm. long, 1-2 mm. broad, glabrous, resinous-punctate. Heads borne at the ends of the branchlets on short pedicels 1-3 mm. long. Involucre turbinate, 4.5-6.0 mm. long, 3.0-4.5 mm. wide; involucral bracts 15 or less, 4-5 mm. long, 1-1.5 mm. wide, glabrous, yellow to yellow-green, with an acute tip, often squarrose. Ligulate flowers 7-12, 2.5-3.5 mm. long, yellow or more frequently white, ligule 2.5-3.5 mm. long, 1.2-1.8 mm. wide; tubular flowers yellow or white, 1.5-2.5 mm. long. Pappus of scales, 0.8-1.5 mm. long in the tubular flowers, 0.5-1.2 mm. long in the ligulate flowers. Achenes 1-2 mm. wide, densely pubescent.

TYPE: Bolivia, prov. Larecaja, "vicinis Sorata," 2,680 m., *Mandon 228* (Isotype GH! US! F! NY!).

DISTRIBUTION: From southern Bolivia to northern Patagonia, and from the foot of the Andes to Tucumán, Córdoba, Sierra de la Ventana (Buenos Aires) and the Atlantic Ocean.

1a. **Gutierrezia mandonii** ssp. **mandonii**

Gutierrezia gilliesii Gris. var. *scabriuscula* Gris., Goett. Abh. **19**:173. 1874; based on Catamarca, unter Nacimientos; Lorentz 434 (Isotype CORD!)

This subspecies is characterized by short leaves, yellow flowers, small campanulate capitula with appressed involucral bracts, and the small globose habit, rarely exceeding 25 cm. tall. The four chromosome counts available indicate that this subspecies is a hexaploid ($n = 12$).

DISTRIBUTION: Southern Bolivia to Tucumán, Argentina. It is found in the valleys ("quebradas") and mountains of the foot of the Bolivian plateau, the Aconquija Mts., and other mountains of the Pampean formation of northern Argentina, between 1,000 and 4,000 m.

SELECTED SPECIMENS: ARGENTINA. PROV. JUJUY. Dept. Yavi: La Quiaca a Villazón, 3,442 m., *Schreiter 10900* (LIL); La Quiaca, 3,450 m., *Meyer 33021* (LIL), *Fidel Zelada* (LIL), *Parodi 9623* (GH). Dept. Cochinoca: Abra Pampa, 3,700 m., *Venturi 9380* (US); Cerro Incahuasi, 4,500 m., *Venturi 10127* (US). Dept. Humahuaca: Tres Cruces, 3,700 m., *Fabris & Marchioni 1801* (US); 20 Km. W. of Humahuaca, 3,600 m., *West 6300* (GH, MO); Mina Aguilar, 4,100 m., *Sleumer 3375* (LIL), *Petersen & Hjerting 101* (LIL); Laguna Colorada, 4,000 m., *Budin 1* (LIL). Dept. Tilcara: Quebrada del Chorro, 2,500 m., *Solbrig 3329* (GH), *Cabrera & Solbrig 16885* (GH, LP), *17023* (GH, LP), *Cabrera 7692* (GH, F, LP); Tilcara, 2,600 m., *Venturi 4853* (GH, A, F, US), *Balls 5951* (US), *Venturi 6221* (US), *6222* (US), *Pereyra 19* (US), *Meyer 33027* (GH, LIL), *Cabrera, Fabris & Marchioni 13288* (US, LP), *Schreiter 10040* (LIL). Dept. Purmamarca: Maimará, 2,500 m., *Solbrig 3325* (GH). Dept. Tumbaya: Volcan, 2,200 m., *Venturi 3411* (US), *Cabrera & Solbrig 16838* (GH, LP); 5 Km. N. of Volcan, 2,200 m., *Solbrig 3335* (GH), *Cabrera & Solbrig 17023* (GH, LP). PROV. SALTA. Dept. Candelaria: Cerro del Chorrillo, 1700 m., *Venturi 3846* (A, US). Dept. Santa Victoria: Lizoite, 3340 m., *Meyer & Bianchi 33033* (GH, LIL). Dept. Poma: Incahuasi, *Cabrera 8218* (GH, F, LP). Dept. Rosario de Lerma, Puerta Tastil, 2,800 m., *Venturi 8156* (GH, A, US, MO, LIL). Dept. Cachi, Cachi Pampa, 3,400 m., *Romero s.n.* (LIL). PROV. CATAMARCA. Dept. Belen: Cuesta de Zapata, 2,000 m., *Cabrera & Solbrig 16749* (GH, LP). Dept. Poman: Cuesta de Poman, *Schickendantz 118* (US). Dept. Capayan: Santo Domingo, *Peirano s.n.* (GH, LIL). Dept. Andalgala, El Suncho, *Jörgensen 1508* (US, GH, MO). PROV. LA RIOJA. Dept. Chilecito, camino a La Mejicana, 2250 m., *Parodi 8061* (GH). Dept. Paganzo: Sierra de Paganzo, *Hunziker, Cocucci & Subils 15859* (CORD). PROV. TUCUMÁN. Dept. Barruyacu: Agua Negra, 1400 m., *Peirano* (GH, A, LIL). Dept. Trancas: Colalao del Valle, 2800 m., *Schreiter 5673* (A, LIL). Dept. Tafi: Tafi del Valle, 2000 m., *J. Hunziker 7160* (GH, BAB), *Lillo 5050* (A, LIL).

BOLIVIA. Dept. Tarija: Puna Patanca, 3800 m., *Fiebrig 2910* (GH, A). Dept. Potosí: Uyuni, *Asplund 4952* (US); Miraflores, 3,600 m., *Cárdenas 4319* (US); west of Chocaya, 3700 m., *West*

6094 (GH, MO); Quechisla, *Cárdenas 53* (GH); near Villazon, 3400 m., *West 8225* (GH, MO): Tupiza, *Fiebrig 3106* (F, GH, US, HBG).

1b. **Gutierrezia mandonii** ssp. **gilliesii** (Gris.) Solbrig, stat. nov. (fig. 31)

Gutierrezia gilliesii Gris., Goett. Abh. **19:** 173. 1874; *G. spathulata* var. *gilliesii* (Gris.) O. Ktze., Rev. Gen. Pl. 3(2): 156. 1898.

Gutierrezia leucantha Cabrera, Rev. Museo de La Plata n.s., Bot. 4: 61. 1941. Based on "Argentina, Buenos Aires, Sierra de la Ventana, entre peñas, *A. L. Cabrera 4475, 23-V-1938*" (Holotype LP!)

This subspecies is characterized by narrow (1 mm.) and long (4–6 cm.) leaves, white flowers (occasionally yellow), turbinate capitula, involucral bracts with green swollen tips, and the large shrubby habit. One population from Córdoba known cytologically is a decaploid ($n=20$), and one from Mendoza is a hexaploid ($n=12$).

TYPE: Argentina. Córdoba, "in collibus ab urbe occidentalibus, in montibus inter S. Pedro et Horcosuni," Lorentz 183 VI-1871. (Isotype CORD! LP!, photo GH!).

Distribution: Central Argentina, from Tucumán to San Luis and Córdoba, in low mountainous areas (less than 1000 m.); Sierra de la Ventana (Prov. Bs. Aires); and La Pampa.

SELECTED SPECIMENS. ARGENTINA. PROV. MENDOZA. Dept. Las Heras: Villavicencio, 1700 m., *Ruiz Leal 8043* (RL), *1040* (RL), *4361* (RL), *8645* (RL), *Burkart, Troncoso & Nicora 14385* (GH, US, SI), *O'Donell 1330* (A, LIL); Papagayos, *Ruiz Leal 4493* (RL); Dept. Lujan: Cerro de Las Cabras, *F. A. Roig* (RL); Arroyo de la Manga, *F. A. Roig* (RL). Dept. Tupungato: Cacheuta, *Solbrig 3396* (GH); Potrerillos, road to Pampa de La Polcura, 2,000 m., *Solbrig 3398* (GH). Dept. San Rafael: San Rafael a Malal-hue, *Lourteig 1020* (US, LIL); Monte Colman, *Ruiz Leal 21724* (RL). PROV. SAN JUAN. Dept. Ullun: Bajada Cuesta Vieja, *Hosseus 2600* (CORD); cumbre Cuesta Nueva, *Hosseus 2540* (CORD); desde Ullun hasta La Angostura, 1800 m., *Hosseus 2517* (CORD). PROV. SAN LUIS. Dept. San Antonio: Quebrada de los Bueyes, *Galander s.n.* (CORD); Sierra de las Quijadas, *Hunziker & Cocucci* 16380 (CORD); Bajo del Jume, *Guiñazú 8* (US). PROV. LA PAMPA. Dept. Lihuel Calel: cerro Lihuel Calel, *Burkart 15960* (SI); Sierra de

FIG. 31-32. *Gutierrezia mandonii*. 31. *G. m.* ssp. *gilliesii* near Los Cocos, Cordoba, Argentina; note the dense, globose, branching system; 32. *G. m.* ssp. *isernii* cerro de La Polcura, Mendoza, Argentina, app. 3,000 m. altitude; note the flattter growth, and the much less developed branch system, probably an adaptation to the high altitude and winter snow.

Lihuel Calel, *Schwabe & Fabris 2002* (LP); Anzoategui, *O'Donell 1767* (LIL); Rio Colorado, *O'Donell 1628* (LIL). PROV. CÓRDOBA. Dept. Santa Maria: Malagueño, *Hunziker 6658* (CORD, LIL, A, GH, US, MO), *O'Donnell & Rodriguez 323* (LIL, F). Dept. Punilla: Sierra Chica, *Lossen 223* (GH); Los Cocos, *Cabrera 6390* (LP, GH, US, F). Dep. Ischillin: Ongamira, *Solbrig 3403* (GH); San Pedro Norte, *Solbrig 3402* (GH). Dept. Pocho: Sierra de Pocho, faldeo E., *Hunziker 13643* (CORD). Dept. Sobremonte: cerca de La Plaza, *Hunziker 12137* (CORD); Sierra de Copacabana, faldeos NE, *Hunziker 14801* (CORD). PROV. BUENOS AIRES. Partido Tornquist: valley south of Pico Ventana, *Bartlett 20036* (GH); Sierra Ventana, *Lorentz s.n.* (GH, US). Partido de Patagones: Carmen de Patagones, *Krapovickas 2012* (LIL).

1c. **Gutierrezia mandonii** ssp. **isernii** (Phil.) Solbrig, stat. nov. (fig. 32)

Brachyris isernii Phil., Anal. Univ. Chile **27**: 337. 1865.

Gutierrezia isernii (Phil.) Phil. Anal. Univ. Chile **87**: 427. 1894.

Subspecies *isernii* is characterized by stiff branches and heads borne solitarily or in groups of 2 or 3 at the ends of the branches. This subspecies is closely related to ssp. *gilliesii*, ssp. *isernii* being smaller (15-30 cm.) than ssp. *gilliesii* and with wider leaves (1-2 mm.). From ssp. *mandonii* it can be separated by the longer leaves and larger capitula (4.5-6.0 mm. long, 3-4.5 mm. wide). The flowers are usually yellow in ssp. *isernii*, but populations with yellow and white flowered plants are known. No cytological information is available on this subspecies.

TYPE: Argentina, "inter St. Rosa et Mendoza," Philippii 1868/69. (SANT!, Isotype LP!).

DISTRIBUTION: Argentina, Mendoza, in the precordillera between 2,000 and 3,000 m.

SELECTED SPECIMENS: ARGENTINA. PROV. MENDOZA. Dept. Tunuyan, Corte Amarillo, *Ruiz Leal 2991* (RL), *3020* (RL); en la precordillera a 2,500 m., *Ruiz Leal 1125* (RL); cerro de la Polcura, *Solbrig 3400* (GH); Los Arboles, *Ruiz Leal 1699* (RL); Quebrada del Arroyo Grande, *Ruiz Leal 13125* (RL); Cuchilla de los Alazanes, *Ruiz Leal 2020* (RL). Dept. Las Heras, Cerro de la Cal, *Carette s.n.* (RL); Pampa Seca, 2,400 m., *Ruiz Leal 5133* (RL); en lomadas, 2,600 m., *Semper s.n.* (RL).

2. **Gutierrezia repens** Griseb., Goett. Abh. **19:** 173. 1874

Rhizomatous, low, slightly creeping, woody, perennial, up to 10 cm. tall, forming mats 10-30 cm. in diameter, branching from the base. Rhizome 5-10 cm. long, 3-8 mm. in diameter, woody. Branches short, 5-15 cm. long, 2-5 mm. in diameter, black or dark gray in color, woody, densely leafy to the top; in older plants only the dried-up petiole-bases remaining. Leaves lanceolate to slightly oblanceolate, 15-35 mm. long, 2-4 mm. wide, acute, petioled, glabrous, resinous-punctate. Capitula borne singly at the ends of leafy flowering branches, that may be undivided or branched, and then with a head at the end of each branchlet. Involucre campanulate, 5-8 mm. long, 7-8 mm. wide; involucral bracts 20 or less, 4-8 mm. long, 2-3.5 mm. wide, oblong, with a broadly acute or obtuse apex, glabrous, resinous, coriaceous, usually yellow-brown in color. Ligulate flowers 10-20, yellow, tube 2-3.5 mm. long, ligule 3.5-7 mm. long, 1.5-3 mm. broad; tubular flowers 15-30, 3-6 mm. long; pappus of scales 1-1.8 mm. long; achenes 1-2 mm. long, 0.5 mm. wide, pubescent.

TYPE: Argentina. Tucumán, "in jugo montis supra Cienaga," 30-III-1872, *P. G. Lorentz 150* (Isotype CORD!).

DISTRIBUTION: This species is endemic to the mountains of Tucumán and adjacent areas of Salta and Catamarca in Argentina, at altitudes between 2,800 and 4,000 m.

SELECTED SPECIMENS: ARGENTINA. PROV. CATAMARCA. Dept. Andalgalá: Cerro del Medio, 3,700 m., *Jörgensen 1366* (GH, UC, LIL, SI, US, MO); valle del Rio Bolson, 4,000 m., *Rohmeder* (LIL); Capillitas, *Schickendantz 96* (CORD). PROV. TUCUMÁN. Dept. Tafi: Cumbre del Chorro, 3,300 m., *Venturi 4117* (A, LIL, SI, US); Pabellon, *Castillon 36* (LIL); Tafi del Valle, *Castillon 620a* (LIL); Real del Derrumbado, 3,800 b., *Venturi 4253* (LIL); Infiernillo, arriba del rancho de Felipe Diaz, 3,500 m., *Sleumer 1989* (LIL); Cerros Calchaquies, *Castillon 2776* (LIL); Cumbre del Malamala, 3,300 m., *Lillo 3471* (LIL), *2722* (LIL), *3453* (LIL); La Cienaga, 2,500-3,300 m., *Schreiter 900* (LIL), *Descole 1614* (LIL), *Sleumer 292* (LIL), *Lillo 3605* (LIL), *3721* (LIL), *3605* (LIL); Lara, 3,200 m., *Lillo s.n.* (LIL); Cumbre del Lara, 4,000 m., *Schreiter 1338* (LIL); Cerro Muñoz, 3,000 m., *Monetti 283* (LIL), *Schreiter 1330* (A, LIL); Cuesta entre Tafi y Malamala, 2,800 m., *Lillo 4348* (LIL); Chasquivil, Potrero Grande, *Lillo 1924* (LIL); Loma del

Diablo, 2,900 m., *Rodriguez 457* (A, LIL, SI), *Lillo 11312* (LIL). Dept. Chicligasta: La Cascada, *Meyer 14129* (LIL); Est. Las Pavas, Puesto El Bayo, 3,300 m., *Venturi 3113* (A, LIL, SI, US), *4651* (LIL); Est. Santa Rosa, 3,500 m., *Meyer 15086* (LIL). Dept. Trancas, Abra de la Quenoa, 2,900 m., *Bellanio 283* (LIL); La Cascada a Las Cuevas, 3,000 m., *Meyer 14888* (LIL). PROV. SALTA. Dept. Trancas: Camino Cuesta del Arca, Trancas, *C. Spegazzini* (LPS 16824).

3. **Gutierrezia ruiz-lealii** Solbrig, spec. nov.

Suffrutex compactus, erectus, 10-25 cm. altus; caulibus parce ramosis, glabris, 25 cm. longis. Folia lanceolata 15-30 mm. longa, 2-4 mm. lata, sessilia, margine integerrima, glandulosa. Capitula ad apicem ramulorum solitaria, vel 2-3, sessilia vel brevissime pedunculata. Involucrum hemisphaericum, 5-7 mm. altum, 6-8 mm. crassum; bracteis 15-20, pluriseriatis, subaequilongis, latissime triangulatis, acutis, 2-3 mm. latis, 5-7 mm. longis; flores marginales 10-14, uniseriales, feminei, ligulati, lutei, tubulo 1.5-2.5 mm. longo, ligula 5-7 mm. longa, 1.5-3 mm. lata; flores disci 12-20, lutei, hermaphroditi, corolla tubulosa 2-4 mm. longa, quinquedentata; squamae papposae aequilongae, 2-3 mm. longae; achaenia pubescentia 1-3 mm. longa, 0.5-1 mm. lata.

Compact, globose subshrub, 10-25 cm. high, from a strong, woody taproot, branching from the base. Root-crown 1-3 cm. in diameter, woody, with dark, grey, thick, fissured bark, usually dichotomously or trichotomously branched. Branches arising in great numbers from the root-crown, up to 25 cm. long, with a woody, thick, grey base, 3-5 cm. long, 5-10 mm. thick, leafless, abruptly changing into the green, semi-woody stems, 1-3 mm. thick, usually undivided, leafy throughout, internodes 5-15 mm. long. Leaves lanceolate, 15-30 mm. long, 2-4 mm. wide, acute, glabrous, glandular-punctate, sessile. Capitula borne at the ends of the branches or seldom in groups of two. Involucre campanulate 5-7 mm. high, 6-8 mm. wide; involucral bracts 15-20, broadly triangular, 2-3 mm. wide, 5-7 mm. long, green, with a well-marked triangular tip of darker color. Ligulate flowers 10-14, yellow, tube 1.5-2.5 mm. long, ligule 5-7 mm. long, 1.5-3 mm. wide; tubular flowers 12-20, 2-4 mm. long; pappus of scales 2-4 mm. long; achenes 1-3 mm. long, 0.5-1 mm. wide, pubescent. FIG. 33-34.

Fig. 33-34. *Gutierrezia ruiz-lealii*, on cerro Horqueta, near Volcán, Jujuy, Argentina, at app. 3500 m. altitude. 33. View of plant. 34. Close-up view. Note the broad leaves, semi-creeping habit, large head and buds.

TYPE: Argentina. Prov. Jujuy, Dept. Tumbaya: cerro Horqueta, cerca de Volcan, 3,500 m., *A. L. Cabrera and O. T. Solbrig 16695* (Holotype GH!, Isotype LP! US! SI!).

DISTRIBUTION: Known so far only from five localities, all above 3,000 m., in Jujuy and Salta, on relatively humid mountain tops.

MATERIAL STUDIED: ARGENTINA. PROV. SALTA. Dept. Santa Victoria: Santa Victoria, 3,340 m., *Meyer and Bianchi* (LIL); Cuesta del Obispo, 2,500-3,000 m., *Meyer 12068* (LIL), *12072* (LIL), *12071* (LIL). Dept. Caldera, Cuesta del Carancho, arriba del Potrero del Castillo, ca. 3,200 m., *Sleumer and Vervoost 2890* (LIL, US); Dept. San Antonio de los Cobres, camino a Mina Concordia, *Cabrera y Schwabe 56* (BAB).

Gutierrezia ruiz-lealii is a very distinct species on account of the large heads, the long yellow ligules and the broad leaves (for a *Gutierrezia*). It is closest to *G. repens*, from which it differs principally in the globose, cushion-like habit of growth, and the smaller leaves. It gives me great pleasure to dedicate this species to Dr. Adrian Ruiz Leal, the enthusiastic, pioneer botanist of Mendoza, Argentina.

4. **Gutierrezia ameghinoi** Speg.,
Rev. Fac. Agr. La Plata 3: 527. 1897

Gutierrezia paniculata (DC) Phil. var. *patagonica* Speg. Rev. Fac. Agr. La Plata 3:608, 1897; *Gutierrezia brachyris patagonica* Macloskie Rep. Princeton Univ. Exp. Patag. 8:780. 1905 based on, Argentina, "Chubut, *Moyano, 1897*" (LPS 11432!).

Small globose shrub, 10-25 cm. tall, from a strong woody root, branching from the base. Root-crown up to 1 cm. in diameter, woody, with dark grey, thick, fissured bark. Branches up to 25 cm. long with a woody base, up to 5 mm. in diameter; branches leafy throughout, internodes 1-10 mm. long. Leaves linear to lanceolate, 10-20 mm. long, 1-3 mm. wide, acute, glabrous, glandular-punctate, the blade attenuating into a pseudo-petiole, or sessile. Capitula borne on slender pedicels 3-15 mm. long, in groups of 1-8 at the ends of the branches. Involucre campanulate, 5-7 mm. long, 5-7 mm. wide; involucral bracts 15 or less, 4-6 mm. long, 1.5-2.5 mm. wide, broadly oblong, with a broad triangular tip, usually resinous, membranous margins and a glabrous surface, usually yellow or yellow gray in color. Ligulate flowers 7-10, yellow (white occasionally) tube 1.8 mm. long, ligule 3 mm. long, 1.5-2.5 mm. wide; tubular flowers 10-15, 2.5-3.5 mm. long. Pappus of scales 2.5 mm. long in the tubular flowers, 1.5 mm. long in the ligulate ones. Achenes 1-3 mm. long, 0.5-1 mm. wide, pubescent.

TYPE: Argentina. Prov. Santa Cruz "rarissime in pratis glareosis secus Rio Deseado, anno 1894," *C. Ameghino 94* (LPS!).

DISTRIBUTION: Argentina. Eastern Patagonia from Santa Cruz to Rio Negro; central and western Rio Negro, Neuquén, southern Mendoza and San Luis. Found in dry, rocky "pampas" between 1,000 and 2,000 m., and in the coastal areas of the Patagonian plateau, down to sea level.

MATERIAL STUDIED: ARGENTINA. PROV. SANTA CRUZ. Pto. San Julian, *Carette s.n.* (LP); Pto. Deseado, *Carette s.n.* (LP) *Eyerdam, Beetle & Grondona 23871* (SI, MO); s.loc., *C. A. Muello 9078* (SI). PROV. CHUBUT. Peninsula Valdez, *Biraben & Biraben 449* (LP), *454* (LP); Cabo Raso, *Valentin s.n.* (LPS); Rio Chico, *C. Ameghino s.n.* (LPS); alrededores de Golfo Nuevo, *Guarrera s.n.* (LP); Puerto Madryn, *Pennington 70* (CORD), *68* (CORD), *Hicken 63* (SI), *73* (SI); Trelew, *O'Donell 3292* (LIL); Gaiman, *Krapovickas 3880* (LIL); Puerto Piramides, *Hicken & Hauman 58* (SI), *235* (SI); Comodoro Rivadavia, *Hicken & Hauman 94* (SI); 20 Km. al E. de Ulsen, *Soriano 2801* (BAB); cerca de las Chapas, *Soriano 2830* (BAB); travesia Kel-la, *C. Burmeister s.n.* (BAB 2119). PROV. RIO NEGRO. Vicinity of Gral. Roca. *Fisher 29* (GH, SI, MO, F, BM, K), *J. Hirschhorn 163* (LP), *683* (LP); Allen, *O'Donell 1931* (A, LIL); Dique Valcheta, *Meyer 7231* (A, LIL), *7207* (LIL); Nahuel Niyen, *Meyer 7273* (LIL), *7180* (LIL); Puerto San Antonio Oeste, *A. T. Hunziker 4258* (LP), *Gomez 65* (SI), *661* (SI); 85 Km. S. of San Antonio, *Eyerdam, Beetle & Grondona 23533* (SI, UC, MO, GH); Dept. San Antonio, ruta 3, 1160, *Correa, Mendoza & Movia 2470* (BAB); El Bolson, *Rasp 102* (LP); camino de Conesa a San Antonio, *Biraben & Biraben 405* (LP); barrancas del Gualicho, *Maldonado 280* (LP); Rio Colorado, *S. Renato s.n.* (SI). PROV. NEUQUÉN. Antes de llegar a Cerro Negro, *O'Donell 2235* (A, LIL); meseta de los Chihuidos, *Castellanos 20165* (LIL), *20210* (LIL); alrededores de la ciudad de Neuquén, *Castellanos 20137* (LIL), *O'Donell 1893* (A, LIL); Currunco Centro, *Maldonado 713* (LP), *688* (LP); lago Moquehue, *Lagayo 3283B* (LP); 40 Km. S. de Zapala *Lagayo 3322* (LP); Plaza Huincul, al E. de la Barda Negra, *Cabrera 11005* (GH, LP, LIL); Sierra Auca Mahuida, *Fabris 813* (LP, F, US). PROV. MENDOZA. Dept. San Rafael:

los chanares, *Ruiz Leal & Roig 18550* (RL); Santa Elena, 1,700 m., *Ruiz Leal 7333* (RL); El Nihuil, *Reales 2044* (LIL); La Pintada, *Ragonese & Macola* 163 (LP); mina Santa Elena, *Ruiz Leal 7333* (LP). Dept. San Carlos: arroyo Hondo, 1,820 m., *Ruiz Leal 9627* (RL); arroyo Carrizalito, 1,750 m., *Ruiz Leal 7521* (LIL, RL); divisadero del Aguila, *Ruiz Leal 6905* (LP, RL); El Papagallo, 1,600 m., *Araque 1506*(LIL), *Balegno & Palacios 4370* (LIL), *Ruiz Leal 11330* (LIL); Ea. Gaucha, *Boelcke 4021* (LP); Ruta 40, 114 Km. al S. de Tunuyan, *Boelcke, Bacigalupo y Correa 23* (LP). PROV. SAN LUIS. Sierras de San Luis, *Deletay-Guinazu 1625* (BAB).

5. **Gutierrezia spathulata** (Phil.) Kurtz,
Bol. Acad. Nac. Ciencias. Córdoba (Argentina), **13**: 194. 1893
(fig. 35)

Brachyris spathulata Phil., An. Univ. Chile **27**: 336. 1865.

Gutierrezia spathulata (Phil.) Kurtz, var. *ochroleuca* Kurtz, Bol. Acad. Nac. Ciencias, Córdoba, **13**: 186. 1893, based on "Mendoza, inter arroyo Papagayos et arroyo Hondo, 27-XII-1892," *Kurtz 7431* (Holotype CORD!, Isotype LP!).

Small globose shrub, 10-20 cm. tall, from a very strong woody root, branching from the base, occasionally with short stoloniferous branches. Caudex and root crown up to 1 cm. in diameter, woody, with dark grey, thick, fissured bark. Branches up to 15 cm. long, and up to 0.5 cm. thick, leafy throughout; the internodes short and the leaves appressed at the base forming a pseudo-rosette of leaves, more elongate towards the tip of the branches; the upper ⅔ of the branches dies back every year so that an old plant at blooming time is formed by a tight cushion of leaves and branches 3-5 cm. thick, from which several flowering shoots emerge. Leaves spathulate, 5-25 mm. long, 3-8 mm. wide, obtuse, glabrous, resinous-punctate, margins sometimes shortly ciliate, basal leaves in particular often coated with resin. Heads borne on peduncles 1-5 mm. long, 1-5 at the ends of the branches. Involucre turbinate, 4.5-5.5 mm. long, 3.5-5 mm. wide; involucral bracts less than 15, 3.5-4.5 mm. long, 1.5-2 mm. wide, glabrous, acute, margins membranous, coriaceous. Ligulate flowers 5-8, yellow or orange, tube 1.5-2 mm. long, ligule 3-3.5 mm. long, 1.5-2 mm. wide; tubular flowers 9-12, 3 mm. long, yellow or orange; pappus of scales 2-2.5 mm. long in the tubular flowers,

FIG. 35-36. 35. *Gutierrezia spathulata,* in the cordillera of Mendoza (photo Adrian Ruiz Leal); 36. *Gutierrezia baccharoides,* Pampa de La Polcura, Mendoza, Argentina. Note the small size of the plants, and the appressed, mat-forming growth habit.

1-1.5 mm. long in the ligulate flowers. Achenes 1-3 mm. long, 0.5-1 mm. wide, densely pubescent, slightly ridged.

TYPE: ARGENTINA, "prope in La Guardia in prov. Mendoza reperit orn. Max Landbeck." (SANT.! Isotype LP!).

DISTRIBUTION: ARGENTINA, on the eastern slopes of the Andes of southern and central Mendoza, Neuquén, and northern Chubut, between 1,500 and 3,500 m.

SELECTED SPECIMENS. ARGENTINA. PROV. MENDOZA. Dept. Tupungato: Confluencia A.° Novillo Muerto y Los Monteros, 1,740 m., *Roig sn.* (RL 15533). Dept. San Carlos: El Cepillo Nuevo, 1,500 m., *Sanzini 1844* (RL); Quebrada Alavarado, *Ruiz Leal 11330* (RL); entre A.° Cortaderas y A.° Hondo, *Ruiz Leal 11005* (LP, LIL, RL), *7521* (LP); camino Pareditas-El Sosneado, *Boelcke 4150* (LP); El Sosneado, 1700 m., *Carette 354* (SI). Dept. Malahue: Chos Malal, 2,000 m., *Combs 180* (K); Los Colgados, *Ruiz Leal & Roig 16015* (RL); Portezuelo del Viento, *Ruiz Leal 9736* (LIL, RL), *9735* (LIL, RL); Portezuelo del Choique, 2,400 m., *Ruiz Leal & Roig 16079* (RL); La Valenciana, 2,100 m., *Ruiz Leal 7815* (RL); Bardas Blancas, Braun, *1889* (RL); Portillo de la Mareta, 3,500 m., *Kurtz 11971* (CORD); Los Molles, *Kurtz 7369* (CORD); Rodeo Viejo, *Kurtz 7189* (CORD). PROV. NEUQUÉN: Arroyo Toil, 1100 m., *Ruiz Leal & Roig 22416* (LP); alrededores del A.° Chaca-y-co, *Chichi 47* (LP); Corusico, *Dawson 1245* (LP); ruta 40, 25 Km. al S. de Zapala, *Perez-Moreau 3146* (LP, BAB). PROV. CHUBUT: entre Trelew y pie de la cordillera, *Moribeau 7* (LP).

6. **Gutierrezia baccharoides** Sch. Bip., Flora **38**: 115. 1855 (fig. 36)

Gutierrezia hoffmanii O. Ktze. Rev. Gen. 3(2): 156. 1898; *G. baccharoides* Sch. Bip. var. *hoffmanii* (O. Ktze.) Hauman, Anal. Soc. Cient. Arg. **86**: 321. 1918; based on *Moreno and Tonini* 523, "Patagonia" (Isotype NY! LP!, photo of type B!).

Gutierrezia pulviniformis Cabrera, Darwiniana 4: 135. 1940. Based on *Carette s.n.*, I-1916, Mendoza, Dept. San Rafael, Cerro Nevado (LP!).

Small, cushion-forming perennial, subshrub, woody, up to 10 cm. tall, but usually forming hemispheric cushions 3-5 cm. in diameter and 3-5 cm. tall, growing together in groups that form mats up to 50 cm. in diameter, branching from the base. Branches short, 3-6 cm. long, 1-3 mm. in diameter, brown in color, woody, densely leafy to the top; in older specimens only the dried-up petiole-bases remaining. Leaves oblanceolate to spathulate, 5-15 mm. long, 2-5 mm. wide, obtuse or somewhat acute, petiolate, surface glabrous, slightly fleshy, resinous-punctate, margins slightly ciliate, often inrolled. Capitula borne singly at the ends of the leafy undivided branches. Involucre campanulate, 5-6 mm. long, 4-7 mm. wide; involucral bracts less than 15, in three loose series, 4-5 mm. long, 1-2 mm. wide, oblong, yellow, coriaceous, with a broadly acute triangular tip that is usually green, margin membranous and glabrous. Ligulate flowers 6-10, yellow, tube 1.5 mm. long, ligule 2.5 mm. long, 1-1.5 mm. wide; tubular flowers about 10, yellow, 3 mm. long; pappus of scales 0.8-1.5 mm. long; achenes about 1-2 mm. long, turbinate, densely pubescent.

TYPE: Chile, Prov. Magallanes "ad sinum Oazy Harbour, ad terminum accesus maris" Febr., *Lechler* pl. mag. *1241* (K!, Isotype F!, NY!).

DISTRIBUTION: Argentina and Chile. From the high Cordillera of Mendoza to the Straits of Magellan, in alpine, subalpine, or subantarctic environments; in Mendoza it is found between 3,000 and 4,000 m., in Magallanes and Santa Cruz at sea level.

SELECTED SPECIMENS. ARGENTINA. MENDOZA: Pampa de La Polcura, 3,000 m., *Solbrig 3399* (GH, LP, US), *Roig 4204* (GH, RL), *Ruiz Leal 21671* (RL); Potrerillos, canchas de Esqui, 3,000 m., *Cuezzo & Say 2549* (LIL, LP); cerca del nacimiento del arroyo Las Cuevas, 3,200 m., *Ruiz Leal 3128* (LP, LIL, RL); Vallecito, 2,700 m., *Sanzini 1311* (LP, RL); Portezuelo Morado, 3,800 m., *Semper*, 1949 (LP, RL); Portezuelo de Las Osamentas, 3,000 m., *Ruiz Leal 7192* (LP, LIL, RL); Cuicenita, *Carette*, 1907 (CORD). PROV. NEUQUÉN: Cerro Colohuincul, *Comber 1091* (K, LP); Rincon Grande, 1,000 m., *Neumayer 384* (LP); Lago Lagar, *Roth*, 1896 (LP); fuentes del Rio Caleufu; 2,000 m., *Roth*, 1896 (LP). *Mauri, 1897* (LPS); Lago Villarino, *Roth*, 1896 (LP). PROV. RIO NEGRO: s. loc., *Wolffügel 20* (SI). PROV. CHUBUT: Carrenleofu, *Illin s.n.* (LPS 16813); entre Rio Pico y Lago Vintter, *Soriano 3075* (LP, BAB); 20 Km. de Rio Pico en camino a Lago Winter, *Krapovickas 4112* (BAB); lat S. 44° 24′, long 0 71° 22′, *Hogberg*, 1902 (SI, BAB).

PROV. SANTA CRUZ: Puerto San Julian, *Blake 107* (BM, K); San Julian-Rio Deseado, *C. Ameghino*, 1899 (LPS).

CHILE. TIERRA DEL FUEGO: Punta Anegada, *Spegazzini 104* (LP).

This is the most distinct of all species of *Gutierrezia* because of its growth-habit. Nevertheless, it is a polytypic taxon also, and specimens from Mendoza differ in size of plant, size of capitulum, number of flowers, and dimensions of the leaves from specimens from Magallanes. Since the distance separating both localities is about 2,000 Km., and the difference in altitude is over 3,000 m., it is not surprising to find such variations. I have seen enough intermediate specimens from localities lying between the northern and southern extremes mentioned, to convince me that we are dealing with only one taxon. However, the Cordillera of Chubut and Santa Cruz is incompletely known botanically, and more field-work may show that *Gutierrezia baccharoides* is a complex of more than one taxon.

7. **Gutierrezia neaeana** (DC.) Blake,
Contr. U. S. Nat. Herb. **26:** 23. 1930
(fig. 37)

Brachyris neaeana DC., Prodr. **5**: 313. 1836.

Small, fruticose, semiglobose, woody shrub, up to 60 cm. tall, from a strong, woody taproot. Root-crown woody, up to 10 mm. in diameter. Branches all from the root-crown, woody and yellow in color and covered with the bases of dried leaves in their first third; leafy, green, and less woody above; up to 5 mm. in diameter, striate. Internodes short below, longer above, up to 20 mm. in length. Leaves entire, oblanceolate, 15-20 mm. long, 2-3 mm. wide, glabrous, sessile, narrowing towards the base, broadly acute at the tip. Heads borne solitarily at the ends of the branches or in groups of 2-4 on long (10-30 mm.) pedicels; involucres broadly turbinate or campanulate, 5-7 mm. high, and 7-8 mm. wide, with membranaceous margins and tip; ray flowers 9-11, ligulate, yellow, ligule up to 5 mm. long and 2.5 mm. wide; disk flowers 11-13, yellow, 5-6 mm. long; pappus approximately 1.5 mm. long; achenes terete, pubescent, 1-2 mm. long at maturity. FIG. 37.

TYPE: Locality unknown, "Chile or Mexico?", fide De Candolle. *Née leg.* (Microfiche of specimen in De Candolle herbarium!)

DISTRIBUTION: Known only from the type (locality unknown) and one collection from the high Cordillera of Central Chile.

MATERIAL STUDIED: CHILE. PROV. ATACAMA: Dept. Vallenar, Quebrada Alfalfa, 3,500 m., *Johnston 6000* (GH).

FIG. 37. *Gutierrezia neaeana* (*Johnston 6000*, GH). Drawing by Arnold Clapman.

Gutierrezia neaeana was described by De Candolle from material collected by Née of the Malaspina expedition. The type does not have any annotation as to locality, and De Candolle in his description says only "Chile or Mexico?" The plant was redescribed by Blake, who rightly points out that it is not any of the known Mexican species, but also that it has not been collected since in South America. The specimen studied is to my knowledge the only other known collection of the species. It coincides well with the description of De Candolle and the amplified one of Blake, except as to size, the Née specimen being much smaller. Nevertheless, height within a species often varies considerably, particularly in high mountain plants. *Gutierrezia* *neaeana* is characterized by its oblanceolate leaves, broad involucres, and the lax arrangement of the heads at the ends of the branches. It was collected in the high Cordillera east of Coquimbo, a region poorly explored botanically. Johnston tentatively identified it as aff. *copiapina* Phil., but later changed it to *repens* var. nov.? *Gutierrezia copiapina* (= *resinosa)* has much narrower leaves, is bushy and woodier, and is a species of low altitudes. *Gutierrezia repens*, although similar in its foliar characteristics, is a creeping plant found in the Aconquija Mts. of Argentina. Its leaves are also lanceolate rather than oblanceolate as in *G. neaeana*.

The lack of collections of *G. neaeana* (as well as those of *G. espinosae* and others) clearly shows the need for more collecting in the high Cordillera and in northern Chile.

8. **Gutierrezia resinosa** (H. & A.) Blake,
Contr. U. S. Nat. Herb. **26**: 232. 1930
(fig. 43)

Galinsoga resinosa H. & A., Bot. Beechey Voy. 32, 1830; *Bahia resinosa* DC. ex Hook. f. & Jacks., Index Kew. **1**: 264. 1893.

Brachyris paniculata DC., Prodr. **5**: 313. 1836; *Gutierrezia paniculata* (DC.) Gray, Pl. Wright. **2**: 78. 1853 (in text); *Gutierrezia brachyris* Macloskie, Rep. Princeton Univ. Exped. Patag. **8**: 780. 1903-06; based on "in Chili circa Coquimbo" *Gaudichaud* (Microfiche G-DC!)

Odontocarpha poeppigii DC., Prodr. **5**: 72. 1836; based on "Chili, in collibus arid. inter Caucon et Tavolingo," leg. *Poeppig* (photo GH!).

Gutierrezia compacta Phil., Anal. Univ. Chile **87**: 427. 1894; based on "prope La Serena, Jan. 1883," leg. *Phillippi* (SANT!, Isotype LP!)

Gutierrezia laricifolia D. Don, ex Hook. & Arn., Comp. Bot. Mag. **2**: 51. 1836; based on "Coquimbo," leg. Mr. *Calcleugh* (not seen).

Brachyris floribunda Phil., Linnaea **33**: 137. 1864; *G. paniculata* var. *floribunda* (Phil.) Reiche, Anal. Univ. Chile **109**: 23. 1901; based on "prope S. Felipe de Aconcagua, Martio 1863," leg. *Phillippi* (SANT!, Isotype LP!).

Large, woody shrubs, 80-150 cm. tall, with one to several well-developed stems up to 15 mm. in diameter, branching in the upper portion; stems striate, with brown-grayish bark; secondary branches lighter, or greenish, and resinous. Leaves linear to linear-lanceolate, 20-40 mm. long, 1-2 mm. wide, entire, acute, sessile, with entire margins, resinous on both surfaces, but amounts of resin varying with plants and environmental conditions. Heads borne in corymb-like groups at the ends of the branches, each branchlet with 1-5 heads. Involucres turbinate, 6-8 mm. long, 3.5-5 mm. wide, involucral bracts in three loose rows, triangular-lanceolate, coriaceous, yellow, with green tips; ray flowers ligulate, 5-7, yellow or white, ligule 2-3 mm. long, 1-2 mm. wide; disk flowers 8-11, yellow or white, 4-5 mm. long; pappus of awns 2-3 mm. long; achene terete, 2-4 mm. long, pubescent.

TYPE: Chile, Coquimbo (not seen)

DISTRIBUTION: Coastal and interior, extra Andean, central Chile, from Vallenar and Coquimbo south to Santiago and Valparaiso. Locally abundant.

SELECTED SPECIMENS: CHILE. PROV. SANTIAGO: Dept. Santiago: Cerro de La Cruz near Limache, *Solbrig 3395* (GH, US, LP), *3394* (GH, US, LP); *Garaventa 2155* (GH); Limache, *Looser 659* (GH); Dept. Valparaiso: Valparaiso, *Hartwig 39* (GH); Viña del Mar, *Hicken 200* (SI). PROV. COQUIMBO: Dept. Ovalle: Fray Jorge, *Muñoz 229* (GH); Cerrillos de Tamaga, *Worth & Morrison 16418* (MO, GH); 3 Km. N. Empalme ruta a Ovalle, on Santiago-Serena road, *Solbrig 3044* (GH). Dept. Coquimbo, Est. El Tangue, *Solbrig 3041* (GH); lomas de Peñuela, *Solbrig 3031* (GH), *3387* (GH); La Serena, *Barros 111* (LP), *1713* (LP), *Philippi s.n.* (LP). Dept. Rivadavia, Vicuña, *Cabrera 104* (LP); Rivadavia, *Werdermann 173* (GH), *Solbrig 3384* (GH).

Although *G. resinosa* is one of the most distinct species of the genus it has been described six times, and ascribed to five different genera! This is due, no doubt, to the fact that it grows in the area of Chile that was most frequently visited by the early botanical expeditions.

Gutierrezia resinosa is replaced north of its range by *G. taltalensis* and *G. espinosae*, two closely related, and most probably derived species. The area north of Serena is very incompletely known botanically, and it is likely that further exploration will reveal a whole complex of small, isolated populations with distinctive characteristics. Which of these deserve specific status has to be decided from the evidence at hand. At present, I feel it is

FIG. 38-41. Flowering branches of *G. taltalensis* and *G. espinosae* showing extremes of variation in leaf size and shape, and arrangement of capitula. 38. *Gutierrezia espinosae (Johnston 5722,* GH); 39. Id. *(Espinosa, 10-XI-1941,* GH); 40. *Gutierrezia taltalensis (Johnston 5665,* GH); 41. Id. *(Johnston 5533,* GH).

best to recognize only the three named species. Even so, the separation of *G. taltalensis* from *G. espinosae* is not always easy (see figs. 38-41).

9. **Gutierrezia taltalensis** Phil., Anal. Univ. Chile **87:** 426. 1894 (fig. 40, 41)

Gutierrezia copiapina Phil., Anal. Univ. Chile **87:** 425. 1894, based on "prope Chañarcillo invenit orn. *Guillermo Geisse* 1885." (SANT!, Isotype LP!).

Medium to large shrubs, 40-120 cm. tall, from a woody base up to 10 mm. in diameter, branching dichotomously; bark light gray, often with the bases of dried up leaves; secondary branches thinner, leafy, internodes short. Leaves linear to linear-lanceolate, 20-40 mm. long, 1-3 mm. wide, entire, glabrous, resinous, acute, sessile. Flowering heads arranged in tight groups of 3-8, sessile or on short pedicels 1-3 mm. long, or occasionally solitary; involucre broadly turbinate, 5-6 mm. long, 3-5 mm. wide; involucral bracts in three obscure rows, lanceolate, acute, coriaceous, with slightly membranaceous margins, and a darker tip; ray flowers ligulate, 7-10, white or yellow, ligule 3-4 mm. long, 1-2 mm. wide; disk flowers tubular, 10-15, white or yellow, 4-5 mm. long; pappus of awns 1-2 mm. long; achenes terete, 1-3 mm. long, pubescent. FIG. 40, 41.

TYPE: Chile. "Proper Taltal in deserto Atacama, legit *Dr. Lud. Darapsky*" (SANT!).

MATERIAL STUDIED: CHILE. PROV. ANTOFAGASTA: Dept. Taltal, Cerro Perales, ca. 1,000 m. alt., *Johnston 5625* (GH, US); Quebrada de San Ramon, *I. M. Johnston 5150* (GH, US); Posada Hidalgos, *I. M. Johnston 5665* (GH, US): Hills S. E. of Taltal, *I. M. Johnston 5112* (GH); Agua de los Mantos, *I. M. Johnston 5658* (GH, US); Aguada Panulcito, *I. M. Johnston 5472* (GH, US); El Rincon, *I. M. Johnston 5533* (GH, US); Aguada Cachina, *I. M. Johnston 5723* (GH); Aguada de Miguel Diaz, *I. M. Johnston* 5331 (GH); Aguada Grande, *I. M. Johnston 5751* (GH).

10. **Gutierrezia espinosae** Acevedo,
Bol. Museo Hist. Nat. Santiago **24:** 82. 1949
(fig. 38, 39)

Small, woody shrub, 40-50 cm. tall. Primary branches up to 10 mm. in diameter, with a rough, gray bark. Secondary branches woody, rough, with prominent elevated leaf scars, leafy in their upper part. Internodes short, 1-3 mm., the branches covered with a gray to gray-brown bark, never green. Leaves mostly oblanceolate, short and broad, 5-15 mm. long, 3-4 mm. broad, or towards the top in well-developed specimens larger and up to 25 mm. long and 5 mm. broad, acute, sessile, surface scrobiculate (at least when dry) due to the presence of large cavities which house the resin-glands, margin entire, with denticulate trichomes. Heads borne in tight glomerules of 3-5 sessile heads or on very short pedicels, 1-5 mm. long, or occasionally solitary. Involucre broadly turbinate, 5-6 mm. high, 4-6 wide; involucral bracts in about 3 unequal rows, lanceolate, acute, coriaceous, yellow with a green tip; ray flowers ligulate, 7-9, white or yellow, ligule 3-5 mm. long, 1-2 mm. wide; disk flowers tubular 10-15, white or yellow, 4-5 mm. long; pappus of short awns 1-1.5 mm. long; achenes terete, pubescent, 1-3 mm. long at maturity. FIG. 38, 39.

TYPE: Chile. Prov. Antofagasta. Dept. Antofagasta, Quebrada de la Chimba, *Marcial R. Espinosa s.n.*, 10-XI-1941 (SANT! Isotype GH!).

DISTRIBUTION: Chile, from Taltal to Antofagasta, in "Quebradas" and "Aguadas" near the coast, where some humidity is present.

MATERIAL STUDIED: CHILE. PROV. ANTOFAGASTA: Dept. Taltal. Cerro de la Cachina, ca. 14 Km. S. of Aguada Cachina, *I. M. Johnston 5722* (GH, US); Dept. Antofagasta. Cerro Gordo, 35 Km. S. of Antofagasta, alt. 1,000 m., *West 6066* (GH); *La Chimba, Barros 70* (LP), *1354* (LP); Cerro Moreno, *Barros 1319* (LP).

SECTION MEGALOCEPHALA SOLBRIG, sect. nov.

Capitula magna, campanulata, ligula alba. Species typicus, *Gutierrezia gayana* (Remy) Reiche, Anal. Univ. Chile **109:** 22. 1901.

11. **Gutierrezia gayana** (Remy) Reiche,
Anal. Univ. Chile **109:** 22. 1901
(fig. 22, 42)

Odontocarpha gayana Remy, in Gay, Flora de Chile, Laminas, Tabl. 44. 1846; *Brachyris gayana* (Remy) Remy, in Gay, Flora de Chile **4:** 36. 1849.

Globose shrub, 50-100 cm. tall. Stems woody, gray or grayish-yellow, up to 5 mm. in diameter, branching profusely; secondary branches striate, green or green-gray. Leaves linear, 3-5 cm. long, 1-2 mm. wide, entire, glabrous, acute, sessile, very glutinous. Heads borne solitary at the end of the branches. Involucre broadly campanulate, 8-12 mm. high, 8-15 mm. wide; involucral bracts arranged in 2-3 very loose rows, broadly lanceolate, 5-10 mm. long, 3-4 mm. wide, membranous with a thin green tip, up to 3 mm. long. Ray flowers 10-15, ligulate, white, ligule 5-7 mm. long, 3-4 mm. wide; tubular flowers white, 4-6 mm. long; pappus about 1.5 mm. long; achene terete, pubescent, 1-3 mm. long at maturity. FIG. 22, 43.

TYPE: Chile. Tabl. 44, Laminas, Gay, Flora de Chile, 1846.

DISTRIBUTION: Endemic to the dry pre-Cordilleran "pampas" north and east of Serena, Chile.

MATERIAL STUDIED: CHILE. PROV. COQUIMBO: Bajada Cuesta Vineta, 108 Km. from Serena, *Solbrig 3073* (GH), *3072* (GH), *3070* (GH); Llano "El Potrero," 84 Km. from Serena, *Solbrig 3055* (GH); Incahuasi, *Jiles P. 2226* (LP). PROV. ATACAMA: Dept. Huasco. Carretera Panamericana, 35 Km. al S. de Vallenar, *Cabrera 12681* (LP); Id., 30 Km. S. de Vallenar, *Cabrera 12621* (LP);

FIG. 42-43. 42. *Gutierrezia gayana* (Cuesta Viñeta, Coquimbo, Chile); note the large heads of white flowers; 43. *Gutierrezia resinosa*, (near La Serena, Chile). note the erect habit, with very little side branching, and the tendency to form several main, trunk-like branches.

camino a Domeyko, entre 36-40 Km. al S. de Vallenar en la quebrada, *Muñoz & Johnson 2001* (LP). Chile, s. loc., *Gaudichaud 104* (GH), *Gay s.n.* (US, NY).

EXCLUDED SPECIES

Brachyris sectifolia Cessati, Att. Acc. Sci. Nap. **5:** 7. 1871. According to the description this species from Villavicencio, Mendoza, Argentina, has divided and opposite leaves. Although I have not seen type-material this species is probably not a *Gutierrezia*.

Gutierrezia cupressiformis Sch. Bip., Flora **38:** 114. 1855 = **Lepidophyllum cupressiformis** (Lam.) Cassini, Dict. Sci. Nat. **26:** 37.

Gutierrezia ledifolia Griseb., Goett. Abh. **19:** 173. 1874 = **Chiliotrichiopsis ledifolia** (Gris.) Cabrera, Notas Museo La Plata **9:** 244. 1944.

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CHROMOSOME NUMBERS OF CRUCIFERAE

Reed C. Rollins

There has been a steady increase in our knowledge of chromosome numbers of the family *Cruciferae* following the comprehensive paper by Manton (1932). However, the point has scarcely been reached where these data can be put to their maximum usefulness. Many more counts, together with authentic determinations of the taxa involved, supported by voucher specimens, are needed before a new comprehensive evaluation of cytological data on the internal classification of the family is justified.

The problem of generic delineation is an unusually difficult one in the *Cruciferae* (cf. Rollins, 1960, 1962). In some instances, a consistency of chromosome number within genera coupled with differences between related genera are helpful in determining where generic lines of demarkation are rightfully placed. The reliability of any such patterns that emerge will be dependent upon the completeness and accuracy of the chromosome counts. Proper application of these data to solutions of particular problems demands broad considerations of diverse kinds of information which can be convincing only if they are evaluated and presented in considerable detail. Obviously, this is not our present purpose. The following listing of chromosome numbers and the accompanying comments are intended to help in rounding out the needed chromosome data and to highlight some cytologically interesting problems that have turned up in the *Cruciferae* during the past three decades of research on this interesting family.

ACKNOWLEDGEMENTS

The chromosome numbers given have been determined as the opportunity of examining the material has presented itself over a number of years, beginning in the early 1940's. Aside from counts I have made, a number of assistants and colleagues have contributed to the counts listed. Those made in a preliminary way by assistants were verified. The late Dr. L. O. Gaiser made a large number of counts, particularly on root-tip material. More recently, Dr. Otto T. Solbrig has examined and reported on fixations we have acquired. I am particularly indebted to Dr. Solbrig for his interest and help. Fixed material has been contributed by a number of collaborators, especially by Dr. Peter Raven. I wish to thank those who have contributed in any way to this study, particularly Dr. Kuldip R. Khanna, who actively collaborated with me in part of this research. Financial support for portions of this work has been given by the National Science Foundation.

Arabis

A. *crandallii* Robinson
  $2n = 14$: Gunnison Co., Colorado. Ripley and Barneby 10206, GH.
  $2n = 14$: Hinsdale Co., Colorado. Rollins 51165, GH.
A. *crandallii* x A. *Holboellii* Hornem., var. *retrofracta* (Grah.) Rydb.
  $2n = 21$: Gunnison Co., Colorado. Rollins 5194, GH.
A. *demissa* Greene, var. *russeola* Rollins
  $2n = 21$: Sweetwater Co., Wyoming. Rollins & Porter 5134, GH.
A. *divaricarpa* A. Nels
  $2n = 14$: Park Co., Colorado. Rollins & Weber 51290. GH.
  $2n = 14$: Conejos Co., Colorado. W. A. Weber 7845. GH.
  $2n = 14$: Park Co., Montana. Rollins & Porter 51244, GH.
  $2n = 14$: Park Co., Wyoming. Rollins & Porter 51252, GH.
  $2n = 22$: Siskiyou Co., California. J. T. Howell 15193, GH.
A. *drummondii* Gray
  $2n = 14$: Park Co., Colorado. Rollins & Weber 51289, GH.
  $2n = 14$: Park Co., Montana. Rollins & Porter 51246, GH.
  $2n = 14$: Park Co., Wyoming. Rollins & Porter 51250, GH.
A. *fendleri* (Wats.) Greene, var. *spatifolia* (Rydb.) Rollins
  $2n = 14$: Douglas Co., Colorado. Rollins 5147, GH.
A. *holboellii* Hornem., var. *pendulocarpa* (A. Nels.) Rollins
  $2n = 14$: Yellowstone National Park, Wyoming. Rollins & Porter 51281, GH.
A. *holboellii* var. *pinetorum* (Tidestr.) Rollins
  $2n = 21$: Sweetwater Co., Wyoming. Rollins & Porter 5135, GH.
A. *holboellii* var. *retrofracta* (Grah.) Rydberg
  $2n = 14$: Siskiyou Co., California. L. Constance *s.n.*, GH.
  $2n = 14$: Park Co., Montana. Rollins & Porter 51245, GH.
A. *lemmonii* Watson
  $2n = 14$: Park Co., Wyoming. C. L. Porter 5888, GH.
A. *lyrata* L., var. *kamchatica* Fischer
  $2n = 16$: Kurupa River Valley, Arctic Slope of Alaska. Hodgdon 8664, GH.

$2n = 32$: Nixon Mine, Kuskokwim Mts., Alaska. Drury 3380, GH.

A. *perstellata* Braun, var. *ampla* Rollins

$n = 7$: Davidson Co., Tennessee. Rollins, Solbrig, Hilferty & Lloyd 6012, GH.

Polyploidy was firmly established in certain species of *Arabis* by evidence presented earlier (Rollins, 1941). Also, the data showed that $x = 7$ was a common fundamental number in the genus. Mulligan (1964) suggests that all species of *Arabis* exclusively North American have a chromosome number based on $x = 7$, whereas the European and Asiatic species are based on $x = 8$. We have no data contrary to this division but I suspect the correlation is with phylogenetic relationship rather than with geography. It just happens that we do not have counts on any of the exclusively North American species that are obviously related to those of Eurasia. To test the point, counts are needed in such species as *Arabis blepharophylla* H. & A., *A. oregana* Roll., *A. modesta* Roll., *A. aculeolata* Greene, *A. furcata* Wats., *A. Nuttallii* Robins., and *A. crucisetosa* Const. & Roll.

The discovery of apomixis in *Arabis holboellii* Hornem. by Böcher (1951) opened the way to a more reasonable explanation of the inconsistent chromosome numbers in *Arabis* than was available earlier. Where apomixis is operative, triploids and various aneuploid numbers can persist in wild populations without difficulty and several different chromosome numbers within a given species are then not surprising.

There is very good evidence (Rollins, 1946) that interspecific hybridization occurs in *Arabis* and I am convinced that hybridization between taxa at specific and infraspecific levels is widespread in the genus. Hybridization, polyploidy and apomixis undoubtedly operate together to provide several polymorphic groups within the genus.

Taxonomically, the most difficult and puzzling complexes are the following, designated by the name of the species with which other less prominent taxa are associated: (1) the *Arabis holboellii* complex, (2) the *Arabis sparsiflora* complex, (3) the *Arabis divaricarpa* complex, (4) the *Arabis fendleri* complex, (5) the *Arabis lemmonii* complex. Although we do not have direct evidence as yet, it is very probable that all three phenomena (i.e., hybridization, polyploidy and apomixis), occur separately or together to provide the complex patterns of variation found in each complex.

Barbarea

B. orthoceras Ledeb.

$n = 8$: San Luis Obispo Co., California. Breedlove 2030, GH.

This count is in line with that of Mulligan (1964) for the species and of other authors for the genus as a whole. The fundamental number $x = 8$ is well established.

Cakile

C. fusiformis Greene

$n = 9$: Aransas Co., Texas. Rollins & Correll 5964, GH.

C. geniculata (Robins.) Millsp.

$n = 9$: Galveston Co., Texas. Rüdenberg. March, 1966, G.H. Count by L. Rüdenberg.

Previous counts on other species of *Cakile* are from more northerly stations in Europe, Asia and North America. However, all counts agree with a fundamental number of $x = 9$. There is still a major need for studies of variation patterns in populations of *Cakile*. Pobedimova's (1964) recognition of eight species in North America and the West Indies requires a careful evaluation.

Cardamine

C. breweri Watson

$n = 42\text{-}48$: Fresno Co., California. Breedlove 5242, GH.

C. parviflora L., var. *arenicola* (Britt.) Schulz

$n = 22\text{-}24$: Morgan Co., Alabama. Rollins *et al.* 6103, GH.

C. digitata Richardson

$2n = 32$: Umiat, near Colville River, Alaska. Thompson 1217, GH.

Only one of the three determinations given above was wholly satisfactory, that of *C. digitata*. Material of the other two taxa proved to be very difficult and a definitive number could not be settled upon. It is clear that $x = 8$ is a fundamental number in *Cardamine* and that polypoidy is widespread in the genus.

Caulanthus

C. coulteri Watson

$n = 14$: Santa Barbara Co., California. Breedlove 1929, GH.

C. flavescens (Hook.) Payson

$n = 14$: Alameda Co., California. Breedlove 4295. GH.

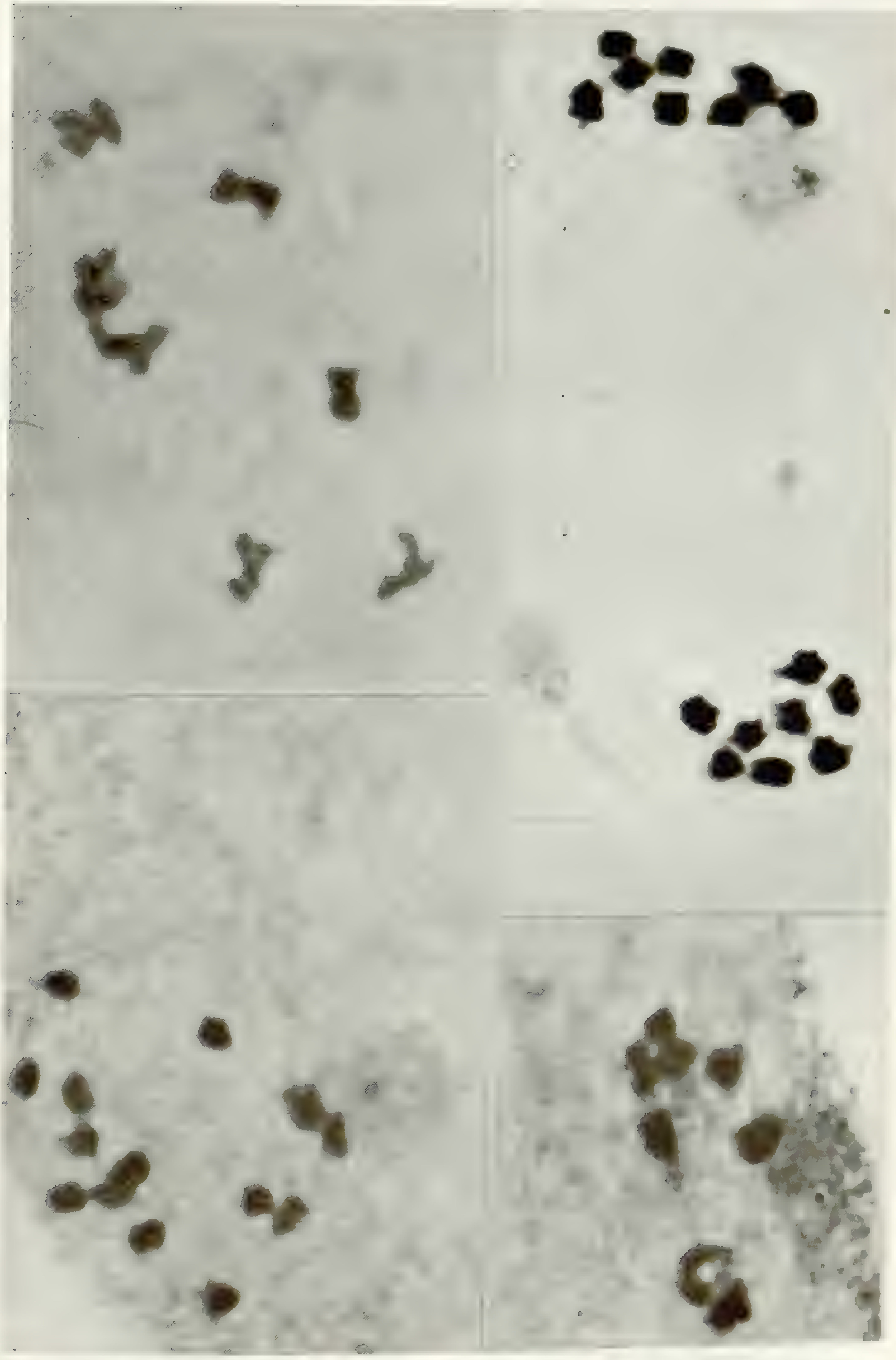

PLATE 1. Upper left, chromosomes of *Lesquerella lasiocarpa*, $n = 7$, Rollins and Correll 5950; upper right, chromosomes of *Lesquerella argyrea*, $n = 8$, Rollins and Correll 5944; lower left, chromosomes of *Caulanthus lemmonii*, $n = 14$, Breedlove 1954; lower right, chromosomes of *Tropidocarpum gracile*, $n = 8$, Breedlove 1822. All figures × 3900.

C. heterophyllus (Nutt.) Payson
  n = 14: San Diego Co., California. Breedlove 1831, GH.

C. inflatus Watson
  n = 10: Kern Co., California. Rollins 4160, DS.
  n = ca. 10: Fresno Co., California. Rollins 4159, DS.

C. lasiophyllus (H. & A.) Payson
  n = 14: Kern Co., California. Breedlove 1951, GH.

C. lasiophyllus var. *inaliens* (Robins.) Payson.
  n = 14 ?: Marin Co., California. Breedlove 4402, GH.

C. lasiophyllus var. *utahensis* (Rydb.) Payson
  n = 14: San Diego Co., California. Breedlove 1859, GH.

C. lemmonii Watson
  n = 14: Kern Co., California. Breedlove 1954, GH. Plate 1.
  n = 14: Monterey Co., California. Breedlove 4312, GH.

The long-standing question as to whether *Caulanthus* should be maintained as a genus distinct from *Streptanthus* is not affected by the chromosome numbers now known. Species in both genera are quite consistently *n* = 14. The exceptions, in addition to *Caulanthus inflatus* given above, are *n* = 12 in *C. crassicaulis* and *Streptanthus cordatus* (Rollins, 1939) and 2*n* = 48 for *Caulanthus lasiophyllus* reported by Snow (1959) under the name *Thelypodium lasiophyllum*. Our findings are different for *C. lasiophyllus*, but this merely suggests a complex chromosome number pattern paralleling a known complex and puzzling taxonomic situation. There is a great need for extensive and detailed studies of *C. lasiophyllus* because of the morphologically divergent plants at present accepted as belonging to this species. The nature and range of variation have not been established. A second known problem involving *C. lasiophyllus* involves its generic placement. Schulz (1924) associated it with a small group of Asiatic species comprising the genus *Microsysimbrium* but this does not seem to be a well founded solution.

The chromosomes of *C. lemmonii* are shown in Plate 1.

Cochlearia

C. groenlandica L.
  2*n* = 14: Prince Charles Island, Canada. W. K. W. Baldwin 1894, GH.

The number 2*n* = 14 is in accordance with numerous counts from Greenland, Canada and Iceland (Saunte, 1955) for this species. The genus has two polyploid series based on x = 6 and x = 7.

Dentaria

D. integrifolia Nuttall
 $n = 16$: Santa Barbara Co., California. Breedlove 1773, GH.
D. integrifolia, var. *californica* (Nutt.) Jepson
 $n = 8$: San Mateo Co., California. Rollins 2947, DS.
 $n = 16$: San Mateo Co., California. Rollins 4196, DS.

The fundamental chromosome number x = 8 is the same for *Dentaria* and *Cardamine* and no evidence is contributed to the problem of whether both of these genera should be recognized or whether all species should be placed in *Cardamine. D. integrifolia* var. *californica* occurs both in open valley swales and on wooded slopes. In a limited area in San Mateo County, California, we found the polyploid in open areas and the diploid on the slopes of the Santa Cruz Mountains. A worthwhile problem for investigation would be to see whether such a correlation is widespread and to determine the significance of such a correlation if it does exist species-wide.

Dithyrea

D. californica Harvey
 $n = 10$: Mohave Co., Arizona. Rollins 4164, DS.
 $n = 10$: San Diego Co., California. Breedlove 1855, GH.
D. wislizenii Engelmann
 $n = 9$, $2n = 18$: Pinal Co., Arizona. Rollins 4168, GH.
 $n = 9$: Presidio Co., Texas. Rollins & Correll 61100, GH.
D. wislizenii, var. *palmeri* Payson
 $n = 9$: Howard Co., Texas. Rollins 53116, GH.

The number $n = 10$ for *D. californica* is the same as that of Lewis (1959) and of Raven *et al.* (1965), and $n = 9$ appears to be a common number in *D. wislizenii.* More counts need to be made on the latter species, especially the annual winter-blooming populations of Arizona. In addition, data from other species of the genus are required before a clear pattern of chromosome numbers will emerge.

Draba

D. glabella Pursh
 $2n =$ ca. 75: Point Jay, Alaska. J. H. Thomas 2297, GH.

D. lanceolata Royle

$n = 16$: Park-Summit Co. line, Colorado. Rollins, Weber & Livingston 5155, GH.

D. oligosperma Nutt.

$2n =$ ca. 60: Albany Co., Wyoming. Ripley & Barneby 10536, GH.

The taxonomy of *Draba* is very confused. This is particularly true of the Arctic and subarctic species and those of high altitudes in the mountains. Chromosome counts on many of the species are high, ranging upward from $n = 16$. A polyploid pattern based on $x = 8$ for *Draba* appears to be emerging but the chromosomes are so small in many instances that it is extremely difficult to obtain a certain count. We have no solid evidence that apomixis occurs in the genus. However, on the basis of the frequent and probably variable chromosome numbers found, it is a fairly safe prediction that apomixis together with interspecific hybridization and polyploidy are responsible for the confused taxonomic picture in the genus.

Erysimum

E. capitatum (Dougl.) Greene

$n = 18$: Contra Costa Co., California. Breedlove 4282, GH.

$n = 18$: Santa Clara Co., California. Breedlove 4673, GH.

E. concinnum Eastwood

$n =$ ca. 18: Marin Co., California. Breedlove 4449, GH.

E. pallasii (Pursh) Fernald

$2n = 36$: Lake Noluk, Brooks Range, Alaska. H. J. Thompson, DS.

Most of the definitive counts made on *Erysimum* indicate a fundamental number of $x = 9$. Our counts on *E. capitatum* are the same as that given by Raven *et al.* (1965) for *E. capitatum* and *E. capitatum* var. *bealianum*. The number $2n = 36$ for *E. pallasii* is in line with other counts in the genus but is somewhat different from an estimated count of $2n =$ ca. 28 by Holmen (1952) for this species. Our count also differs from the counts of $n = 12$ and $2n = 24$ given by Mulligan (1966) for *E. pallasii.*

Eutrema

E. edwardsii R. Brown

$2n = 18$: North slope, Brooks Range, Alaska. Thompson 1342, GH.

Eutrema edwardsii is a widespread species of arctic and subarctic regions occurring on all continents that extend into these high latitudes. It is morphologically variable and also appears to have several chromosome races. The counts of $2n = 28$ and $2n = 42$ by Mulligan (1964) substantiate the same counts by others. Our count of $2n = 18$ introduces a complication that is not at present open to resolution.

Halimolobos

H. perplexa (Hend.) Rollins
$2n = 14$: Adams Co., Idaho. M. Ownbey 3293, GH.

Previous counts (Jørgensen, Sørensen and Westergaard, 1958, Mulligan, 1964) on *H. mollis* agree on $2n = 16$, pointing to a base number of $x = 8$. However, our finding of $2n = 14$ for *H. perplexa* suggests $x = 7$ may be another fundamental number in the genus.

Lepidium

L. densiflorum Schrader
$n =$ ca. 16: Morgan Co., Alabama. Rollins *et al.* 6115, GH.
L. jaredii Brandegee
$n = 8$, $2n = 16$: San Benito Co., California. Wiggins & Rollins 18, GH.
L. perfoliatum L.
$n = 8$: White Pine Co., Nevada. Breedlove 5814, GH.
L. strictum (Wats.) Rattan
$n =$ca. 16: Santa Cruz Co., California. Breedlove 4635, GH.

Lepidium continues to check out as "a very uniform polyploid genus," as suggested by Manton (1932) in her early paper on the cytology of the *Cruciferae*. *L. jaredii* is a very distinct localized species of California and it is interesting to find that its chromosome number conforms to the pattern otherwise known in the genus.

Leavenworthia

Reference is made to table 1, pages 9 & 10, Contributions from the Gray Herbarium No. 192, 1963, where a detailed listing of chromosome numbers is given. The numbers $n = 11$, $n = 15$ and $n = 24$ are found in the genus. No new counts have been made.

Lesquerella

L. *alpina* (Nutt.) Watson, var. *spathulata* (Rydb.) Payson
  $2n = 12$: Custer Co., South Dakota. Ripley & Barneby *s.n.*, GH.
L. *angustifolia* Nuttall
  $n = 5$: Choctaw Co., Oklahoma. Rollins 5971, GH.
  $n = 5$: Choctaw Co., Oklahoma. Rollins 6151, GH.
L. *arenosa* (Richards.) Rydberg
  $2n = 18$: Custer Co., South Dakota. Ripley & Barneby 10559, GH.
L. *argyrea* (Gray) Watson
  $n = 6$: Victoria Co., Texas. Rollins 5361, GH.
  $n = 7$: Victoria Co., Texas. Rollins 5566, GH.
  $n = 7$: South of Saltillo, Coahuila, Mexico. Rollins & Tryon 58121, GH.
  $n = 8$: Kennedy Co., Texas. Rollins & Correll 5961, GH.
  $n = 8$: Webb Co., Texas. Rollins & Correll 5944, GH. PLATE 1.
  $n = 9$: Uvalde Co., Texas. Rollins & Correll 5942, GH.
  $n = 12$: Refugio Co., Texas. Rollins 5359, GH.
  $n =$ ca. 15: Refugio Co., Texas. Rollins 5564, GH.
  $n = 16$, $n = 17 \pm 1$: Webb Co., Texas. Rollins & Correll 5946, GH.
  $n = 18$: Llano Co., Texas. Rollins 53104 and 53105, GH.
L. *arizonica* Watson
  $n = 5$: Mohave Co., Arizona. Rollins 4167, GH.
L. *auriculata* (Engelm. & Gray) Watson
  $n = 8$: Comanche Co., Oklahoma. Rollins 53123, GH.
  $n = 8$: Grady Co., Oklahoma. Rollins 53126, GH.
L. *densiflora* (Gray) Watson
  $n = 7$: Llano Co., Texas. Rollins 53103, GH.
  $n = 7$: Llano Co., Texas. Rollins 5574, GH.
  $n = 7$: Gillespie Co., Texas. Rollins 53106, GH.
  $n = 7$: Dewitt Co., Texas. Rollins 5560, GH.
L. *densipila* Rollins
  $n = 8$: Williamson Co., Tennessee. R. & D. Rollins 5215, GH.
  $n = 8$: Williamson Co., Tennessee. Rollins 5315, GH.
  $n = 8$: Williamson Co., Tennessee. Rollins 53137, GH.
  $n = 8$: Marshall Co., Tennessee. Rollins 5321, GH.
  $n = 8$: Marshall Co., Tennessee. Rollins 53140, GH.
  $n = 8$: Rutherford Co., Tennessee. Rollins 55124, GH.

$n = 8$: Maury Co., Tennessee. Rollins 55146, GH.
$n = 8$: Morgan Co., Alabama. Rollins & Chambers 5710, GH.
$n = 8$: Morgan Co., Alabama. Rollins 5924, GH.
$n = 8$: Morgan Co., Alabama. Rollins *et al.* 6105, GH.
$n = 8$: Lawrence Co., Alabama. Rollins *et al.* 6127, GH.

L. densipila × *L. lescurii*
$n = 8$ Cheatham Co., Tennessee. Rollins 5326, GH.
$n = 8$ Cheatham Co., Tennessee. Rollins 53130, GH.
$n = 8$ Williamson Co., Tennessee. Rollins 5325, GH.
$n = 8$ Williamson Co., Tennessee. Rollins 53135, GH.

L. engelmannii (Gray) Watson
$n = 18$: Guadalupe Co., Texas. Rollins 5366, GH.

L. fendleri (Gray) Watson
$2n = 12$: Brewster Co., Texas. B. H. Warnock *s.n.*, GH.
$n = 6$: Howard Co., Texas. Rollins 53117, GH.
$n = 6$: Jeff Davis Co., Texas. Rollins 53114, GH.
$n = 6$: South of Saltillo, Coahuila, Mexico. Rollins & Tryon 58131, GH.
$n = 12$: Andrews Co., Texas. Rollins & Correll 61149, GH.

L. filiformis Rollins
$n = 7$: Dade Co., Missouri. Rollins 61158, GH.

L. globosa (Desv.) Watson
$n = 7$: Davidson Co., Tennessee. Rollins 5312, GH.
$n = 7$: Davidson Co., Tennessee. Rollins 53132, GH.
$n = 7$: Davidson Co., Tennessee. R. & D. Rollins 5213, GH.
$n = 7$: Maury Co., Tennessee. Rollins & Quarterman 55150, GH.

L. gordonii (Gray) Watson
$n = 6$: Baylor Co., Texas. Rollins 53120, GH. PLATE 3.
$2n = 12$: Brewster Co., Texas. B. H. Warnock *s.n.*, GH. PLATE 2.

L. gracilis (Hook.) Watson
$n = 6$: Lowndes Co., Mississippi. Rollins *et al.* 5644, GH.
$n = 6$: Bryan Co., Oklahoma. Rollins 5970, GH.
$n = 6$: Ellis Co., Texas. Rollins 5347, GH.
$n = 6$: Kaufman Co., Texas. Rollins 5343 and 5344, GH.
$n = 6$: Leon Co., Texas. Rollins & Correll 5968, GH.
$n = 6$: McLennan Co., Texas. Rollins 5349, GH.
$n = 6$: Williamson Co., Texas. Rollins 5554, GH.

L. gracilis var. *repanda* (Nutt.) Payson
$n = 6$: Cotton Co., Oklahoma. Rollins 53121, GH.

L. *grandiflora* (Hook.) Watson
  $n = 9$: Austin Co., Texas. Rollins 5352, GH.
  $n = 9$: Austin Co., Texas. Rollins & Correll 5965, GH.
  $n = 9$: Dewitt Co., Texas. Rollins 5561, GH.
  $n = 9$: Gonzales Co., Texas. Rollins 5363, GH.
  $n = 9$: Wilson Co., Texas. Rollins 5364 and 5365, GH.
L. *intermedia* (Wats.) Heller
  $2n = 18$: Garfield Co., Utah. Rollins 51200, GH.
L. *lasiocarpa* (Hook. ex Gray) Watson
  $n = 7$: Cameron Co., Texas. Rollins & Correll 5950, GH. PLATE 1.
L. *latifolia* A. Nelson
  $n = 5$; $2n = 10$: Clark Co., Nevada. Clokey 8358, DS.
L. *lescurii* (Gray) Watson
  $n = 8$: Cheatham Co., Tennessee. Rollins 53131, GH.
  $n = 8$: Davidson Co., Tennessee. Rollins 53127, GH.
  $n = 8$: Davidson Co., Tennessee. R. & D. Rollins 5209, GH.
  $n = 8$: Rutherford Co., Tennessee. Rollins 55174, GH.
  $n = 8$: Williamson Co., Tennessee. Rollins 53136, GH.
  $n = 8$: Williamson Co., Tennessee. Rollins 55111, GH.
L. *lindheimeri* (Gray) Watson
  $n = 6$: Refugio Co., Texas. Rollins 5562 and 5563, GH.
  $n = 6$: Victoria Co., Texas. Rollins 5360, GH.
  $n = 6$: Victoria Co., Texas. Rollins 5565, GH.
L. *ludoviciana* (Nutt.) Watson
  $2n = 10$: Moffat Co., Colorado. Rollins & Porter 5115, GH.
L. *lyrata* Rollins
  $n = 8$: Franklin Co., Alabama. Rollins 5547 and 5548, GH.
  $n = 8$: Franklin Co., Alabama. Rollins *et al.* 5599, GH.
  $n = 8$: Franklin Co., Alabama. Rollins 55188, GH.
L. × *maxima* Rollins *(L. densipila × stonensis)*
  $n = 8$: Davidson Co., Tennessee. Rollins *et al.* 5222, GH.
  $n = 8$: Davidson Co., Tennessee. Rollins 5313 and 53142, GH.
L. *mcvaughiana* Rollins
  $2n = 12$: Brewster Co., Texas. Warnock & Turner 8646, GH.
  $2n = 12$: Pecos Co., Texas. B. H. Warnock *s.n.*
L. *ovalifolia* Rydb., var. *alba* Goodman
  $n = 6$: Caddo Co., Oklahoma. Rollins 53125, GH.
  $n = 6$: Comanche Co., Oklahoma. Rollins 53124, GH.
L. *palmeri* Watson
  $n = 5$: Pima Co., Arizona. J. Poindexter 1, DS.

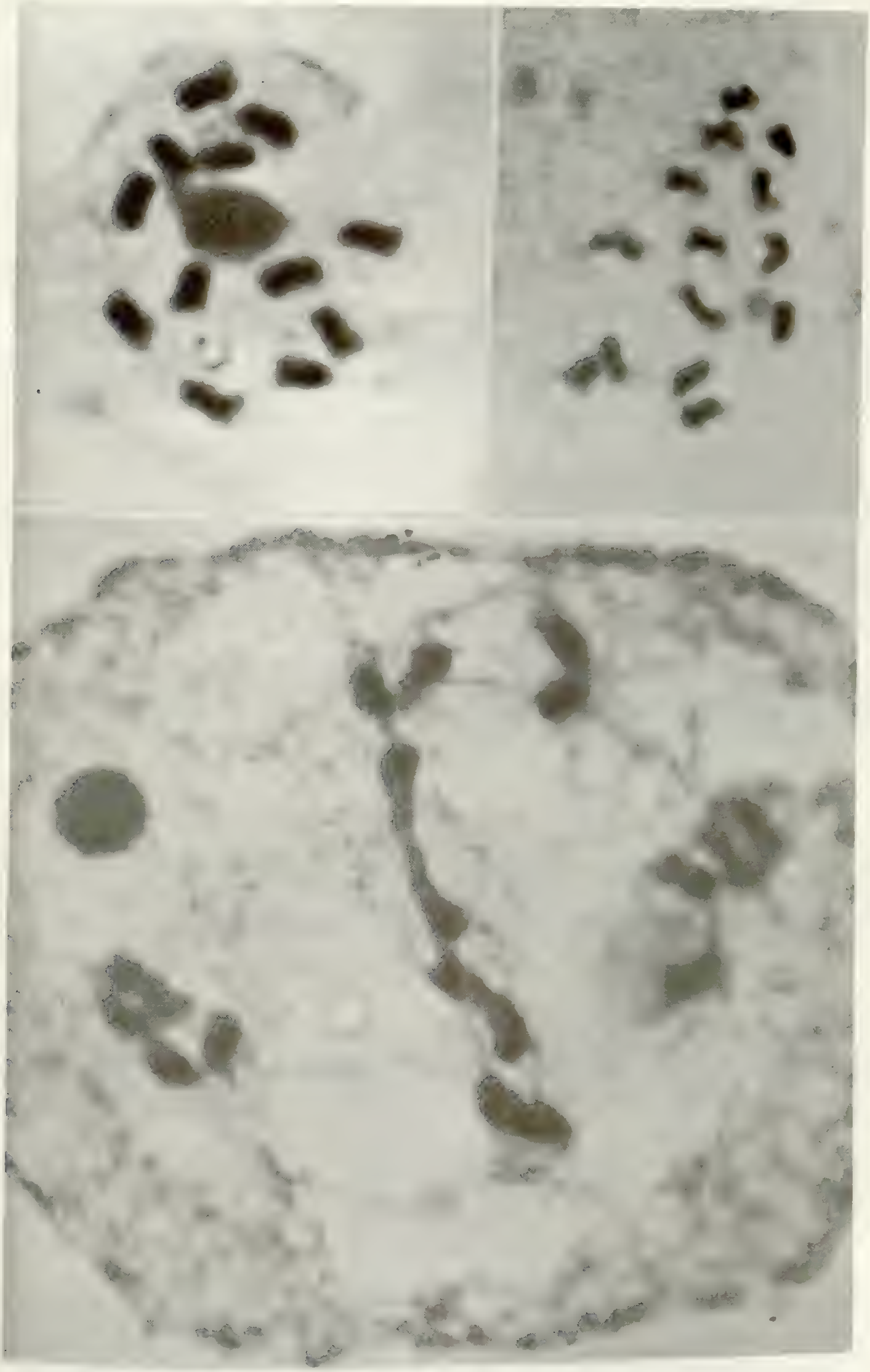

PLATE 2. Upper left, chromosomes in a tapetal cell of *Lesquerella gordonii*, $2n = 12$, Warnock *s.n.*; upper right, chromosomes of *Streptanthus cutleri*, $n = 14$, Rollins and Correll 61111; lower, chromosomes of *Lesquerella purpurea*, $n = 9$, Rollins and Correll 61117. All figures × 3900.

L. perforata Rollins

$n = 8$: Wilson Co., Tennessee. R. & D. Rollins 5207, GH.

$n = 8$: Wilson Co., Tennessee. Rollins 5304, 5306 and 53145, GH.

L. purpurea (Gray) Watson

$n = 9$: Brewster Co., Texas. Rollins & Correll 6181, GH.

$n = 9$: Hudspeth Co., Texas. Rollins & Correll 61117, GH. PLATE 2.

$n = 18$: Val Verde Co., Texas. Rollins & Correll 6160, GH.

L. recurvata (Engelm.) Watson

$n = 5$: Comal Co., Texas. Rollins 5387, GH.

$n = 5$: Gillespie Co., Texas. Rollins 53101, GH.

$n = 5$: Sutton Co., Texas. Rollins 53110, GH.

L. sessilis (Wats.) Small

$n = 6$: Gillespie Co., Texas. Rollins 53100; 53107 and 53109, GH.

$n = 6$: Kimble Co., Texas. Rollins & Correll 5937, GH.

L. stonensis Rollins

$n = 8$: Rutherford Co., Tennessee. Rollins 55177, GH.

L. subumbellata Rollins

$2n = 10$: Uintah Co., Utah. Rollins & Porter 5119, GH.

L. wardii Watson

$2n = 12$: Piute Co., Utah. Rollins 51221, GH.

Most species of *Lesquerella* have chromosomes large enough to work with beyond that of merely counting them. However, we have not had cytological study as a goal in itself, hence no attempts have been made to characterize individual chromosomes or genomes.

An aneuploid series of chromosome numbers between species extends unbroken from $n = 5$ through $n = 9$. Fundamental numbers appear to include $x = 5$, $x = 6$, $x = 7$, $x = 8$ and $x = 9$ and there are polyploid species or populations based on $x = 6$ and $x = 9$. Polyploids based on $x = 6$ include *L. arenosa*, $2n = 18$; probably *L. argyrea*, $n = 18$, from Llano Co., Texas; *L. engelmannii*, $n = 18$; *L. fendleri*, $n = 12$, one count from Andrews Co., Texas and *L. intermedia*, $2n = 18$.

The polyploid population of *L. purpurea*, $n = 18$, from Val Verde Co., Texas, appears to be based upon $x = 9$.

The most complex chromosome number situation so far encountered in *Lesquerella* occurs in *L. argyrea*. The taxonomy of what must at present be termed the "*L. argyrea* complex" is not at all clear. There may be several taxa present instead of one. Further, it is fairly certain that natural hybridization is a factor in producing the complex taxonomic pattern found.

Excellent chromosome number integrity based on $x = 8$ is shown by the majority of the group of related annual species bearing auriculate cauline leaves (Rollins, 1955). The one certain exception is *L. grandiflora* with $n = 9$. *L. lasiocarpa*, rather doubtfully to be associated in the same subgeneric grouping, has $n = 7$.

High chromosome numbers have been reported for taxa at extremes of the distribution range of *Lesquerella* if the early report of Manton (1932) is taken at face value. Her report for *L. mendocina* was $2n =$ ca. 50. The one fact that raises a question in this case is that the species is attributed to Chile and the seed is supposed to have come from a wild plant. If one relies only on undisputed evidence, *Lesquerella* does not occur in Chile, thus making this particular count slightly open to question. On the other hand, counts of $n = 30$ and $2n = 60$ (cf. Jørgensen *et al.* 1958) seem well established for *L. arctica*.

The chromosomes of *L. argyrea* and *L. lasiocarpa* are shown in PLATE 1, those of *L. gordonii* and *L. purpurea* in PLATE 2, and of *L. gordonii* in PLATE 3.

Lyrocarpa

L. coulteri Hooker & Harvey

$2n = 20$: Pinal Co., Arizona. Nichol 23, US.

Raven (1959) presented a count of $n = 20$ for *L. coulteri* var. *palmeri* (as *L. palmeri*). As far as I am aware, only two counts have been made in the genus. Polyploidy is obviously present but it would be unsafe to make any assumptions as to the fundamental number for the genus without further evidence.

Nerisyrenia

N. camporum (Gray) Greene

$n = 9$: Brewster Co., Texas. Rollins & Correll 6180, GH.

$n = 11$: Torreon-Saltillo, Coahuila, Mexico. Rollins & Tryon 58293, GH.

N. linearifolia (Wats.) Greene

$n = 9$: Culberson Co., Texas. Rollins & Correll 61144, GH.

We now have three separate chromosome numbers for *N.*

camporum, $n = 7$ (Rollins, 1939a) and the two given above. Plants identified as *N. camporum* form extensive populations at frequent intervals from trans-Pecos Texas and New Mexico far to the South and West in the Chihuahuan Desert of Mexico. The variation present is extensive and puzzling. The differing chromosome numbers is a clue that suggests sexual reproduction is not strictly adhered to throughout the species. The possibility that several taxa are being masked by the presently accepted taxonomy has to be considered also.

Physaria

P. acutifolia Rydberg

$2n = 8$: Gunnison Co., Colorado. Ripley & Barneby 10200, GH.

P. australis (Pays.) Rollins

$2n = 8$: Boulder Co., Colorado. Rollins 5145, GH.

$2n = 10$: Uintah Co., Utah. Rollins 3091, GH.

$2n = 14$: Albany Co., Wyoming. Ripley & Barneby 10543, GH.

P. chambersii Rollins

$2n = 10$: Emery Co., Utah. Rollins 51183, GH.

P. chambersii, var. *membranacea* Rollins

$2n =$ ca. 20. Garfield Co., Utah. Rollins 51207, GH.

P. oregona Watson

$2n = 8$: Idaho Co., Idaho. Ripley & Barneby 10729, GH.

Earlier (Rollins, 1939b) it appeared that the chromosome numbers in *Physaria* would be straightforward, based on $x = 4$. At least, this assumption could be made if the first three counts of three different species were indicative of the broader picture in the genus. The count of $n = 8$ for *P. vitulifera* (Weber and Brewbaker, 1950) did not disturb the assumption that $x = 4$ is the fundamental number even though polyploidy was then established in the genus. However, the presently reported counts show that a more complex situation exists in *P. australis* than was shown earlier, and it is clear from counts of *P. chambersii* that $x = 5$ must also be a fundamental number in the genus. This does not take into account the odd number of $2n = 14$ in *P. australis* from Albany Co., Wyoming, which shows no relationship to the other counts.

Rorippa

R. *curvipes* Greene
  $n = 8$: Gunnison Co., Colorado, Rollins 51172, GH.
R. *curvisiliqua* (Hook.) Bessey
  $n = 8$: Josephine Co., Oregon. Constance & Rollins 2943, GH.
R. *sinuata* (Nutt.) A. S. Hitchcock
  $n = 8$: Thomas Co., Kansas. Rollins 5101, GH.
R. *subumbellata* Rollins
  $n = 5$: Eldorado Co., California. Rollins 3027, GH.

The fundamental number $x = 8$ has become well established in *Rorippa* with most of the recent counts merely confirming and extending earlier records. A polyploid series exists but deviations from a multiple series were not recorded prior to the present count of $n = 5$ for *R. subumbellata*. This disturbance of an otherwise consistent chromosome number pattern in the genus is anomalous and the significance of it is not known.

Selenia

S. *aurea* Nuttall
  $n = 23$: Garland Co., Arkansas. Rollins & Chambers 5756, GH.
S. *grandis* Martin
  $n = 12$: Dimmit Co., Texas. Barclay 706, GH.

Selenia grandis grows very well under greenhouse conditions and we were able to sample the material repeatedly for reassurance of an accurate count. Material of *S. aurea* was fixed in the field. These first known counts for the genus suggest polyploidy. The disrupted ranges of most of the species provide a basis for an evolutionary pattern that could prove to be exceedingly interesting. This is a genus that deserves careful re-study even though it was the relatively recent subject of a paper by Martin (1940).

Sibara

S. *pectinata* Greene
  $n = 14$: Desierto Viscaino Region, Baja California, Mexico. Gentry 7396, GH.
S. *virginica* (L.) Rollins
  $2n = 16$: Marshall Co., Tennessee. Sharp *et al.* 11188, GH.

Of the two previous counts in *Sibara* (Rollins, 1947) $2n = 26$ for S. *desertii* and $2n = 28$ for S. *viereckii*, the latter fits with the count for S. *pectinata*. The other two counts show little relationship to each other or to the $n = 14$ number. All species of *Sibara*, except S. *virginica*, are limited in distribution and are infrequently collected. It will probably take many years to resolve what is at present a puzzling series of chromosome numbers in the genus.

Sisymbrium

S. *altissimum* L.
  $n = 7$: Lake County, California. Breedlove 5134, GH.
S. *linearifolium* (Gray) Payson
  $n = 11$: Las Animas Co., Colorado. Rollins 1818, GH.
  $n = 11$: Brewster Co., Texas. Rollins & Correll 6168 and 6139, GH.
S. *linifolium* Nuttall
  $n = 7$: Albany Co., Wyoming. Rollins & Porter 5113, GH.
  $n = 8$: Uinta Co., Wyoming. Rollins 1773, GH.
S. *orientale* L.
  $n = 7$: San Diego Co., California. Breedlove 1816, GH.

The two counts for the introduced species, S. *altissimum* and S. *orientale* are the same as those of most other European species of *Sisymbrium*. S. *linifolium* appears to fit the same pattern but the count discrepancy of $n = 7$ and $n = 8$ may have some significance. This species is morphologically very variable and the infraspecific taxonomy requires intensive study for a better understanding than is now available. The very different count of $n = 11$ for S. *linearifolium* lends support to taxonomic treatments that place this species outside of *Sisymbrium*.

Stanleya

S. *pinnata* (Pursh) Britton, var. *integrifolia* (James) Rollins
  $n = 14$: Brewster Co., Texas. Rollins 6191, GH.

The count of $n = 14$ does not accord with my previous counts (Rollins, 1939c) which indicated $x = 12$ as the fundamental number for *Stanleya*. On the other hand, $n = 14$ fits an emerging $x = 14$ that is widespread in *Caulanthus*, *Thelypodium* and *Strepthanthus*, genera somewhat related to *Stanleya*.

Strepthanthella

S. *longirostris* (Wats.) Rydberg
$2n = 28$: Sweetwater Co., Wyoming. Rollins & Porter 5144, GH.
S. *longirostris*, var. *derelicta* J. T. Howell
$n = 14$: San Diego Co., California. Breedlove 1865, GH.

Although *Streptanthella* is usually given the status of a monotypic genus in current manuals and floras, it is by no means certain that this is the correct taxonomic interpretation. It is probable that the one species, S. *longirostris*, should be associated with such species as *Caulanthus cooperi* but perhaps not in the genus *Caulanthus*. The chromosome number does not contribute anything toward solving the problem.

Streptanthus

S. *barbiger* Greene
$n = 14$: Lake Co., California. Breedlove 5145, GH.
S. *breweri* Gray
$n = 14$: Colusa Co., California. Breedlove 5181, GH.
$n = 14$: Napa Co., California. Breedlove 5088, GH.
S. *carinatus* Wright
$n =$ ca. 14: Brewster Co., Texas. Rollins & Correll 6178, GH.
$n = 14$: Presidio Co., Texas. Rollins & Correll 61105, GH. PLATE 3.
S. *cordatus* Nuttall
$n = 12$: Mohave Co., Arizona. Rollins 4166, GH.
S. *cutleri* Cory
$n = 14$: Brewster Co., Texas. Rollins & Correll 61111, GH. PLATE 2.
S. *diversifolia* Watson
$n = 14$: Fresno Co., California. Breedlove 5270, GH.
S. *glandulosa* Hooker
$n = 14$: Lake Co., California. Breedlove 5158, GH.
$n =$ ca. 14: Santa Clara Co., California. Breedlove 4986, GH.
S. *insignis* Jepson
$n = 14$: Monterey Co., California. Breedlove 2375, GH.
$n = 14$: San Benito Co., California. Wiggins & Rollins 24 and 34, GH.

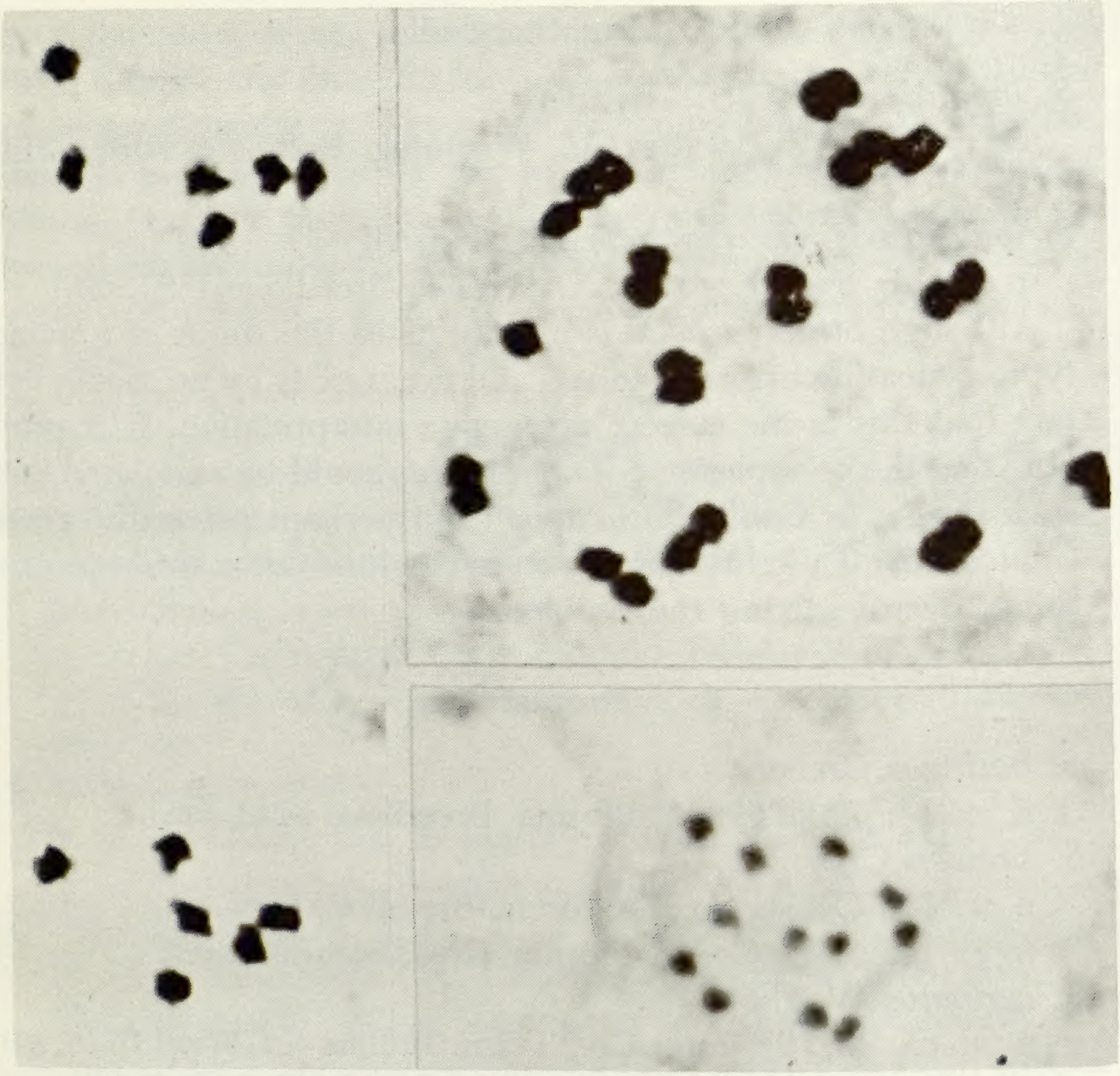

PLATE 3. Left, chromosomes of *Lesquerella gordonii*, $n = 6$, Rollins 53120; upper right, chromosomes of *Streptanthus carinatus*, $n = 14$, Rollins and Correll 61105; lower right, chromosomes of *Selenia grandis*, $n = 12$, Barclay 706. All figures × 3900.

S. *niger* Greene
  $n = 14$: Marin Co., California. Breedlove 4962, GH.
S. *secundus* Greene
  $n = 14$: Sonoma Co., California. Constance & Rollins 2863, GH.
S. *tortuosus* Kellogg
  $n = 14$: Siskiyou Co., California. Constance & Rollins 2901, GH.
  $n = 14$: Tuolumne Co., California. Breedlove 4830, GH.

There is near uniformity of the chromosome number $n = 14$ in *Streptanthus*. The known exception is S. *cordata* with $n = 12$. Further counts are needed in the group to which S. *cordatus* belongs. The species involved were segregated from *Streptanthus* and placed in the genus *Cartiera* by Greene (1906) and by Schulz (1936). The one count pointed to here suggests the possibility of chromosome number support for such a separation. However, the uniformity elsewhere in *Streptanthus* does not support a wholesale breaking up of the genus as attempted by Greene (l.c.) and followed by Schulz (l.c.).

Chromosomes of S. *cutleri* are shown in PLATE 2. Those of S. *carinatus* are shown in PLATE 3.

Synthlipsis

S. *greggii* Gray
n = 10: Northeast of Durango, Durango, Mexico. Rollins & Tryon 58280, GH.

This is the first count in *Synthlipsis*. The three known species (Rollins, 1959) are found mainly in Mexico.

Thelypodium

T. *flavescens* (Hook.) Watson
n = 14: Monterey Co., California. Breedlove 2180, GH.
T. *flexuosum* Robinson
n = 13: Harney Co., Oregon. Raven 18452, GH.
T. *laciniatum* (Hook.) Endlicher, var. *milleflorum* (A. Nels.) Payson
n = ca. 14: Eureka Co., California. Raven 18533, GH.
T. *laciniatum*, var. *streptanthoides* (Leiberg) Payson
n = ca. 12: Grant Co., Washington. Raven 18487, GH.
T. *lemmonii* Greene
n = 14: San Benito Co., California. Wiggins & Rollins 36, GH.
T. *texanum* (Cory) Rollins
n = 13: Brewster Co., Texas. Rollins & Correll 6188, GH.
n = 13: Brewster Co., Texas. Rollins & Correll 6176, GH.

A relatively high fundamental number (or numbers) is emerging for *Thelypodium*. This finding is in general accord with the presence of similar numbers in related genera such as *Stanleya* and *Caulanthus*. The counts given for T. *laciniatum* are tentative because good figures for counting could not be found in the material available for study.

Thlaspi

T. fendleri Gray

$2n = 14$: Mt. Ord, Brewster Co., Texas. B. H. Warnock *s.n.*, GH.

$2n = 28$: Hinsdale Co., Colorado. Rollins 51107, GH.

T. glaucum A. Nelson

$2n = 14$: Douglas Co., Colorado. Rollins & Livingston 5148, GH.

T. parviflorum A. Nelson

$n = 7$: Sheridan Co., Wyoming. Williams 3092, GH.

Thlaspi is widely distributed in the Northern Hemisphere but also occurs sparingly in temperate areas of the Southern Hemisphere. The genus is relatively well-marked and is readily distinguishable from others of the family. The chromosome number too is relatively uniform, based on $x = 7$. Our material shows polyploidy to be present in *T. fendleri*.

Tropidocarpum

T. gracile Hooker

$n = 8$: San Diego Co., California. Breedlove 1822, GH.

$n = 8$: Santa Barbara Co., California. Breedlove 1904, GH.

Thysanocarpus

T. curvipes Hooker

$n = 7$: Humboldt Co., California. Constance & Rollins 2884, GH.

T. elegans Fischer & Meyer

$2n = 28$: San Luis Obispo Co., California. M. P. & A. G. Vestal *s.n.*, GH.

Manton (1932) gave a count of $2n = 28$ for *T. curvipes*. If all identifications are correct, this means polyploidy is present within *T. curvipes*. The presence of $2n = 28$ in *T. elegans* proves that multiple chromosome numbers are present in the genus, at least. The taxonomy of *Thysanocarpus* is very much in need of a careful study and revision.

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