THE SYSTEMATICS OF THE GENERA SABAZIA SELLOA AND TRICARPHA (COMPOSITAE)

By

Edwin Keith Longpre

AN ABSTRACT OF A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
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ABSTRACT

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The genera Sabazia, Selloa and Tricarpha of the family Compositae, tribe Heliantheae, subtribe Galinsogineae are perennial and annual herbs of montane habitats native chiefly to Mexico. The range of Sabazia, however, extends into the Cordillera Oriental of Colombia. Cytological, anatomical and morphological evidence of the generic relationships requires the transfer of Sabazia and Selloa from the subtribe Verbesininae to the Galinsogineae. The genus Tricarpha is described as new and assigned also to the subtribe Galinsogineae.

Ten species and five additional varieties are recognized in Sabazia. Two of these species, S. leavenworthii and S. microspermoides are described for the first time. Sabazia sarmentosa var. lancifolia, S. liebmannii var. hintonii and S. liebmannii var. ovatifolius are recognized as new varieties. Three species, S. multiradiata, S. trianae and S. acoma are transferred from Calea. The genus Selloa comprises two species, S. plantaginea and S. obtusata, the latter of which is transferred from Sabazia. The genus Tricarpha is established to accommodate a species formerly

in Sabazia which is now recognized as T. purpusii, and one new species, T. durangensis. Two other species are excluded from Sabazia and referred to Galinsoga.

Chromosome numbers of seven Sabazia species have been determined, three of these for the first time. The genus includes one diploid, three tetraploid, one octoploid and two duodecaploid species. The basic chromosome number of Sabazia is x = 4. Chromosome counts for the two species of Selloa are reported for the first time as n = 8. Results of crossing studies in Sabazia reveal what appear to be strong genetic barriers, as evidenced by only three sterile F_1 hybrids obtained from thirteen attempted crossing programs involving seven taxa.

Comparative anatomical studies of ray and disc florets, phyllaries, pales, stems and leaves have disclosed basic histological patterns with varied exceptions depending upon the organ or taxon.

The origins of Sabazia and Selloa are thought to have occurred in the Mexican transvolcanic belt because that area is the center of diversity for the group and the most primitive species are found there. Distribution of populations in both northern and southern directions was probably achieved by dispersal from one mountain range to another during the late Tertiary and Pleistocene. Geographical isolation, polyploidy and hybridization appear to have been significant factors in the evolution of Sabazia.

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I should also like to thank the curators of the following herbaria for the loan of specimens: Dudley Herbarium, Stanford University (DS); Field Museum of Natural History (F); Gray Herbarium, Harvard University (GH); University of Michigan (MICH); Missouri Botanical Garden (MO); Michigan State University (MSC); New York Botanical Garden (NY); University of Texas (TEX); University of California, Berkeley (UC); U. S. National Museum (US).

TABLE OF CONTENTS

Table of Contents (continued)

Table of Contents (continued)

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

The major natural subunits or tribes of the Compositae were first recognized by Henri Cassini in 1819. Although the details of his tribal classification have been modified by later investigators, its major outlines have been retained and are still considered to represent mostly natural alliances within the family. On the other hand, the greatest difficulties in classification in the Compositae are encountered at the subtribal, generic and specific levels. Lack of understanding at these levels may be attributed to scarcity of critical material, the complexity of evolutionary modifications, and the frequent overemphasis of certain technical characters. As a result, various subtribes and genera of the Compositae are still poorly defined concepts which do not accurately represent evolutionary relationships.

This investigation was initially designed as a monographic study of the genus Sabazia, but during the investigation it became evident that two closely related genera, Selloa and Tricarpha, were so intimately involved that they could not be ignored. Consequently, it has been necessary to re-examine the generic criteria which apply to this group of the Compositae and to re-evaluate the subtribal position of these genera in view of the confusion which exists con-

cerning their placement in the family. In addition to these objectives, an attempt has been made to study interspecific relationships within Sabazia, Selloa, and Tricarpha.

One reason for taxonomic problems in Sabazia is the sporadic occurrence of the pappus in various species. Shinners (1946) and De Jong (1965) have also noted this problem in Chaetopappa and Astranthium, respectively. In Sabazia the presence or absence of a pappus has affected not only the classification and recognition of species but also has added to difficulties in characterizing the genus and assigning it to the proper subtribe.

Sabazia is native to Mexico, Central America and Colombia with the majority of species concentrated in Mexico. It is generally confined to montane areas above 2000 meters in open forests or subalpine meadows. Selloa is indigenous to southern Mexico and northern Guatemala, and is ecologically similar to Sabazia in being restricted to high elevations and being associated with open pine forests. One species of Tricarpha is native to the western continental slope of Durango and is montane in habitat; the other is endemic to the Cape region of Baja California.

During three months of field work I have examined eight of the fifteen taxa of Sabazia and both species of Selloa in their native habitats. The studies of Tricarpha are limited to herbarium specimens. A biosystematic approach utilizing cytology, genetics, anatomy and morphology was

employed in treating the taxa of Sabazia which were collected in the field. Likewise, this approach was also used in Selloa, notwithstanding the omission of crossing studies.

This treatment of Sabazia, Selloa, and Tricarpha is by no means conclusive. Further biosystematic investigations of the taxa in the field would be most desirable in supplementing knowledge of evolutionary relationships. Despite the continuing lack of information concerning certain aspects of the genera, it is hoped that the present treatment will be of value in properly defining their limits, and will provide a classification which reflects their evolutionary history more accurately than has previously been the case.

HISTORICAL ACCOUNT

The genus Sabazia was established by Cassini in 1827 on the basis of Sabazia humilis, a species previously described by Humboldt, Bonpland, and Kunth as Eclipta humilis. According to Cassini, the origin of the generic name was of no particular significance, having been derived from the name of the Greek god Bacchus. The second species of Sabazia, S. sarmentosa, was described by Lessing in 1830. Two species, S. urticaefolia and S. microglossa, published by De Candolle in 1836 are excluded from Sabazia in this study and are referred to Galinsoga.

The fifth species, Sabazia liebmannii, was described by Klatt in 1887. Its name was derived from the nomen nudum Tridax liebmannii of Schultz Bipontinus, and is synonymous with S. liebmannii. Sabazia michoacana, which was published by Robinson in 1892 and which is recognized in this treatment as a variety of S. liebmannii, was the last of six species included in the only revision of the genus, that by Robinson and Greenman (1904).

Since the revision of Sabazia in 1904, seven additional taxa have been described: S. anomala by Greenman in 1905, and four species (including two varieties) by Blake from 1924 to 1942. In the present treatment, fifteen taxa are recognized (ten species and five varieties). Two species,

Sabazia leavenworthii and S. microspermoides, and three varieties are described for the first time.

The genus Selloa was established by Humboldt, Bonpland and Kunth in 1820 with their description of S. plantaginea. It was named after C. Sello, a German contemporary who owned a herbarium and botanical garden. In 1893 Robinson and Seaton, apparently unaware of the genus, described the conspecific Pringle collection (no. 4226) as Sabazia subnuda.

MATERIALS AND METHODS

Fresh plant material for anatomical studies was killed and fixed in F. A. A. (10 parts 95% ethyl alcohol, 7 parts water, 2 parts 40% formaldehyde, and 1 part glacial acetic acid). Dried material taken from herbarium sheets was restored by immersion in a 3% aqueous sodium hydroxide solution. Flowers for whole mounts were further cleared in a full-strength solution of Clorox. Additional procedures used in making slides of whole mounts and transections follow those outlined by Carlquist (1957). Whole mounts were used exclusively in studying pollen grains while transections were employed in the anatomical investigations of leaves and stems. Both procedures were utilized in the anatomical study of floral organs. Unless otherwise stated the tracing of vascular bundles in whole mounts of ray and disc corollas was based on the presence of tracheary elements. Although this monograph deals with Sabazia, Selloa and Tricarpha, related genera are often cited in the anatomical section for comparative purposes.

Pollen was obtained from the anthers of herbarium specimens. Following washes in water and glacial acetic acid, respectively, the grains were acetolized in a mixture of 1 part concentrated sulfuric acid to 9 parts acetic anhydride in a boiling water bath for one minute. The pollen

was then subjected to two washes of glacial acetic acid and water. The material was next bleached in an aqueous solution of 20% sodium hypochlorite, followed by two washes in distilled water. The pollen grains were stained with Safranin-O for one minute prior to two more washes with distilled water. Afterwards, the spores were washed three times with absolute alcohol, and finally benzene was added to each sample. Dow Corning silicone oil was added to the pollen residue in a vial with a little benzene, and was left standing until the benzene evaporated. A small drop of silicone oil residue was placed directly on a cleaned glass slide. A cover glass was affixed to the slide by a ring of clear fingernail polish completely encircling the cover glass.

All measurements (with the exception of a few taken directly from pollen grains immersed in acetocarmine) were made from silicone-mounted material. According to Andersen (1960), this medium has less effect in promoting spore expansion upon storage than other media such as balsam. The pollen grains were measured with a Zeiss research microscope under a magnification of ca. 1220 X with a calibrated ocular micrometer. Two to six samples of 30 spore diameters each were measured, and an average was ascertained from a total of six slides per taxon. Measurements of spine length were taken from thirty spores from the above samples, with the exception of Sabazia multiradiata and S. sarmentosa var.

lancifolia which were not measured.

Bud collections for studies of chromosome numbers were obtained in the field during the summers of 1961 and 1962. Immediately after the flower buds were collected, they were killed and fixed in freshly prepared Carnoy's colution (6 parts 95% ethyl alcohol, 3 parts chloroform, and 1 part glacial acetic acid). During both field trips the buds were stored in an ice cooler, and upon reaching East Lansing, were stored in a refrigerator at 8 - 10°C. The anthers were squashed and stained employing the acetocarmine smear technique. Drawings were made of meiotic chromosomes with the aid of a Zeiss drawing apparatus under a Zeiss phase-contrast microscope at an initial magnification of cà. 3600 diameters.

All parental species of Sabazia involved in the hybridization program were collected in the field and cultured under greenhouse conditions as well as in a garden in East Lansing under partial shade during the summer. Young flowering heads were self-pollinated using a camel's hair brush for the transfer of pollen, and afterward they were immediately bagged. This procedure was repeated at least six times. Results of these tests showed that seed set was generally absent or of rare occurrence, indicating self-incompatibility. Cross pollination was accomplished by rubbing two flowering heads together which were at an early stage of anthesis, and then they were bagged. This technique was repeated at least every other day until the outer

disc florets began to turn brown and wither. Each cross involved several plants.

Pollen fertility was estimated by obtaining percentages of pollen stainability based on a total of 1000 to 1500 grains per plant. Pollen grains were stained in cotton blue-lactophenol and percentages of pollen stainability were reflected by the number of grains whose nuclei stained dark blue. Meiosis within the F_1 hybrids was studied in the same manner as was described for chromosome studies.

Voucher specimens prepared for anatomical, pollen, chromosomal and crossing studies, have been deposited in the Beal-Darlington Herbarium of Michigan State University. Sources of all special plant materials used in this investigation are listed in Table 1.

Table 1. Source of material used in anatomical, pollen and crossing studies.

taxon	location	collection and herbarium
Calea palmeri	MEXICO: Michoacan	Longpre 113, MSC
Galinsoga hispida	MEXICO: State of Mexico	Pringle 10821, MSC
Galinsoga parviflora	UNITED STATES: Michigan	Longpre 524, MSC
Sabazia acoma	COLOMBIA: Norte de Santander	Killip & Smith 19637, US
S. humilis	MEXICO: Federal District	Beaman 4539, MSC

. . . continued

Table 1 (continued)

taxon	location	collection and herbarium
	MEXICO: State of Mexico	Longpre 350a, MSC
S. leavenworthii	MEXICO: Michoacan	Longpre 105, MSC
S. liebmannii var. liebmannii	MEXICO: Oaxaca	Longpre 293, MSC
S. liebmannii var. ovatifolia	MEXICO: Oaxaca	Longpre 199, MSC
S. mullerae	MEXICO: Nuevo Leon	Longpre 503, MSC
S. multiradiata	MEXICO: Oaxaca MEXICO: Oaxaca	Purpus 3837, F Rose & Hay 5650, US
S. pinetorum	GUATEMALA: Huehuetenango	Longpre 227, MSC
S. sarmentosa var. sarmentosa	GUATEMALA: Huehuetenango MEXICO: Puebla	Longpre 257, MSC Longpre 502, MSC
S. trianae	COLOMBIA: Cundinamarca	Cuatrecasas 281, F.
Selloa obtusata	GUATEMALA: Huehuetenango	Longpre 228, MSC
S. plantaginea	MEXICO: State of Mexico	Longpre 149, MSC
Tricarpha purpusii	MEXICO: Baja Sur	Purpus 3961, NY, US
Tridax balbisioides	MEXICO: Chihuahua	Pringle 769, MSC
Tridax trilobata	MEXICO: State of Mexico	Pringle 4271, MSC
Verbesina liebmannii	MEXICO: Oaxaca	Pringle 4918, MSC

CYTOLOGICAL AND GENETICAL STUDIES

Chromosome Numbers.

Meiotic irregularities were not observed and chromosomal alignment appeared to be normal at metaphase I. Chromosome numbers, which were obtained from cells undergoing microsporogenesis (specifically at diakenesis), are listed in Table 2. Selected configurations are illustrated in Fig. 1.

In the initial cytological investigations of *Sabazia*, Turner and Johnston (1961) reported a chromosome number of $n = 4$ for *S. humilis*. Later studies of Turner *et al.* (1962) and Powell and Turner (1963), respectively, showed that *S. multiradiata* had $n = 8$, and that *S. liebmannii* was characterized by $n = 24$. Counts are now available for seven of the ten species, and all appear to be on a base of $x = 4$. Of the *Sabazia* species studied cytologically, *S. humilis* with $n = 4$, is a diploid annual while the other species are polyploid perennials.

Chromosomal evidence has proven useful in supporting the taxonomic position of varieties and species distinguished chiefly on the basis of anatomical and morphological features. At the varietal level, both *Sabazia liebmannii* var. *liebmannii* and var. *ovatifolia* are characterized by $n = 24$. At

Figure 1. Meiotic chromosomes of *Sabazia* and *Selloa*, X ca. 1800. a. *Sabazia humilis*, *n* = 4 (*Longpre 490*). b. *Sabazia mullerae*, *n* = 8 (*Longpre 503*). c. *Sabazia pinetorum*, *n* = 8 (*Beaman 3801*). d. *Sabazia leavenworthii*, *n* = 16 (*Longpre 105*). e. *Sabazia sarmentosa* var. *sarmentosa*, *n* = 24 (*Longpre 502*). f. *Sabazia liebmannii* var. *liebmannii*, *n* = 24 (*Longpre 293*). g. *Sabazia liebmannii* var. *ovatifolia*, *n* = 24 (*Longpre 199*). h. *Selloa plantaginea*, *n* = 8 (*Longpre 149*). i. *Selloa obtusata*, *n* = 8 (*Longpre 228*).

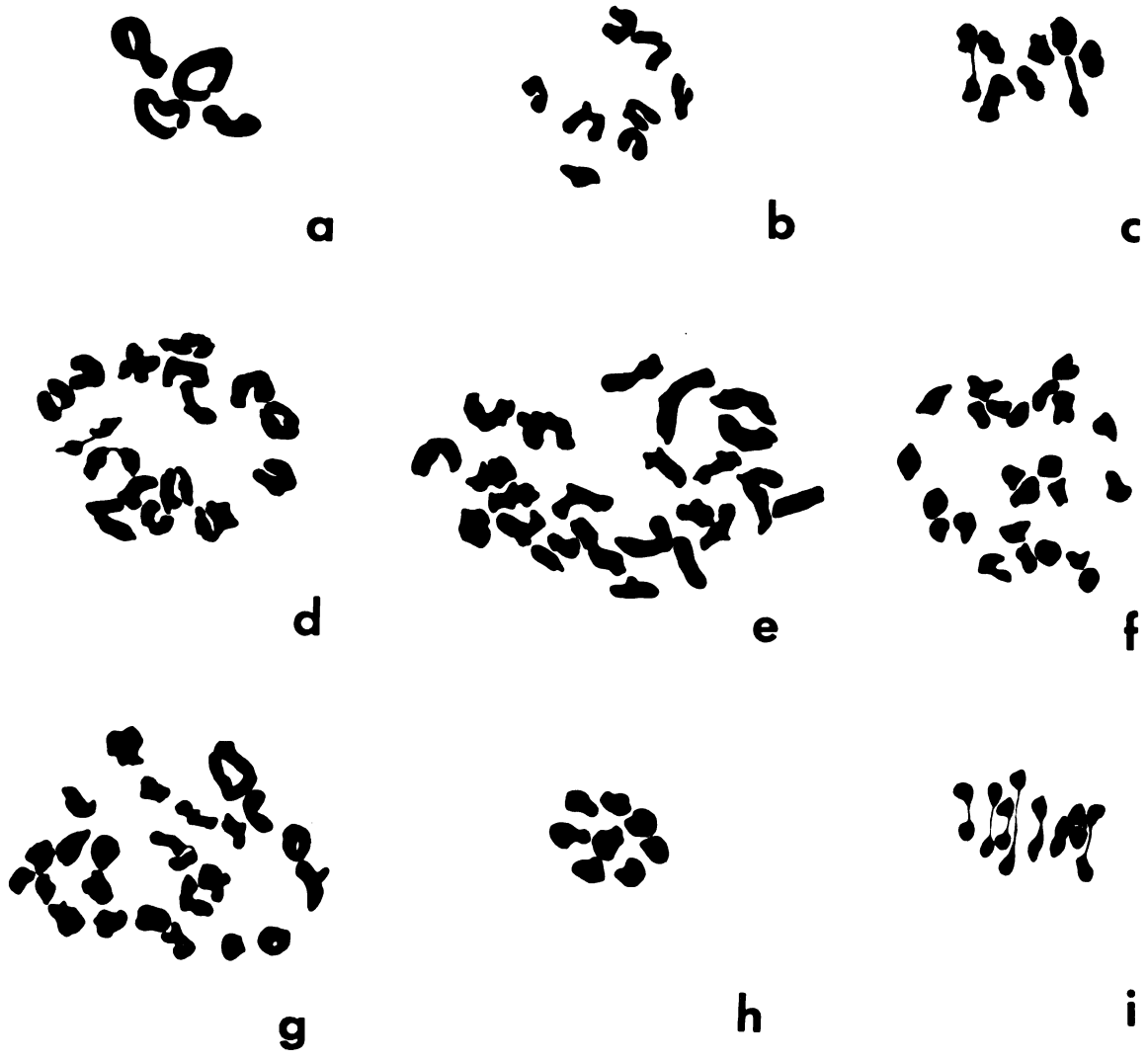

a
b
c
d
e
f
g
h
i

Table 2. Meiotic chromosome numbers in *Sabazia*, *Selloa*, and *Galinsoga*.

taxon	n number	collection or reference
Sabazia humilis	4	Turner and Johnston (1961)
	4	MEXICO: FEDERAL DISTRICT, near La Cima along old Cuernavaca hwy (Rt 95) between Km 43 and 44, *Longpre* 407
	4	MEXICO: FEDERAL DISTRICT, old hwy 190 to La Cima between Km 36 and 37, *Longpre* 419
	4	MEXICO: HIDALGO, along road to Singuilucan 1.9 mi S of hwy 130 junction, *Longpre* 437
	4	MEXICO: STATE OF MEXICO, Nevado de Toluca, *Longpre* 143
	4	MEXICO: STATE OF MEXICO, along hwy 190 from Puebla to Mex City between Km 65 and 66, *Longpre* 350a
	4	MEXICO: STATE OF MEXICO, Nevado de Toluca, N side of mtn at NE side of Loma Alta, *Longpre* 490
S. multiradiata	8	Turner, Powell and King (1962, reported as *Sabazia*)
S. mullerae	8	MEXICO: NUEVO LEON, Cerro Potosi, E side of mtn at Km 18, *Longpre* 503
S. pinetorum	8	GUATEMALA: HUEHUETENANGO, Sierra de los Cuchumatanes, at Km 317.5 on Ruta Nacional 9N, *Beaman* 3801
	8	GUATEMALA: HUEHUETENANGO: Sierra de los Cuchumatanes, at Km 324.5 on Ruta Nacional 9N, *Beaman* 3846

. . . continued

Table 2 (continued)

taxon	n number	collection or reference
	8	GUATEMALA: HUEHUETENANGO, Sierra de los Cuchumatanes on Ruta Nacional 9N between Km 317.5 and 319, Longpre 227
S. leavenworthii	16	MEXICO: MICHOACAN, Tancitaro along trail on eastern slope of mtn, Longpre 105
S. sarmentosa var. sarmentosa	24	GUATEMALA: HUEHUETENANGO, Sierra de los Cuchumatanes along Ruta Nacional 9N between Km 326 and 327, Longpre 257
	24	MEXICO: PUEBLA, Honey, along wet stream bank E of train station, Longpre 502
S. liebmannii var liebmannii	24	Powell and Turner (1963)
	24	MEXICO: OAXACA, on the Oaxaca-Valle Nacional hwy 25 mi W of Ixtlan, Beaman 3661
	24	MEXICO: OAXACA, along hwy 190 between Km 498 and 499, 29.7 mi N of Oaxaca, Longpre 293
S. liebmannii var. ovatifolia	24	Powell and Turner (1963, reported as S. michoacana)
	24	MEXICO: OAXACA, along hwy 190 between Km 422 and 423, ca 47 miles NW of Oaxaca, Longpre 199
Selloa plantaginea	8	MEXICO: STATE OF MEXICO, at Puerto del Aire on the Mexico-Puebla hwy 54.5 Km E of Mex. City, Beaman 2904
	8	MEXICO: STATE OF MEXICO, Nevado de Toluca, 1.4 mi beyond turnoff to crater, Longpre 149

. . . continued

Table 2 (continued)

taxon	n number	collection or reference
Selloa obtusata	8	GUATEMALA: HUEHUETENANGO, Sierra de los Cuchumatanes, Beaman 3845
	8	GUATEMALA: HUEHUETENANGO, Sierra de los Cuchumatanes, between Km 322 and 323, Longpre 228
Galinsoga parviflora	8	Covas and Schnack (1946)
	8	Haskell and Marks (1952)
	8, 16	Turner, Powell and King (1962)
	16	MEXICO: FEDERAL DISTRICT, Univ. of Mexico campus, Longpre 177

the specific level, S. multiradiata, S. mullerae and S. pinetorum are closely related, sharing similar morphological and anatomical features in addition to having n = 8. Sabazia sarmentosa and S. liebmannii, with n = 24, may have originated from an ancestral hybrid complex from S. multiradiata (n = 8) and S. leavenworthii (n = 16). This possibility is discussed further in the systematic section under the respective species.

Galinsoga, which approaches Sabazia through S. humilis, has been reported to have chromosome numbers of n = 8 and n = 16 (Turner et al. 1962). This haploid condition has

been verified through the Mexican collection of Galinsoga parviflora (Longpre 177). Stenocarpha filiformis, which should be classified between Sabazia and Galinsoga according to Turner (1965), is also characterized by n = 8.

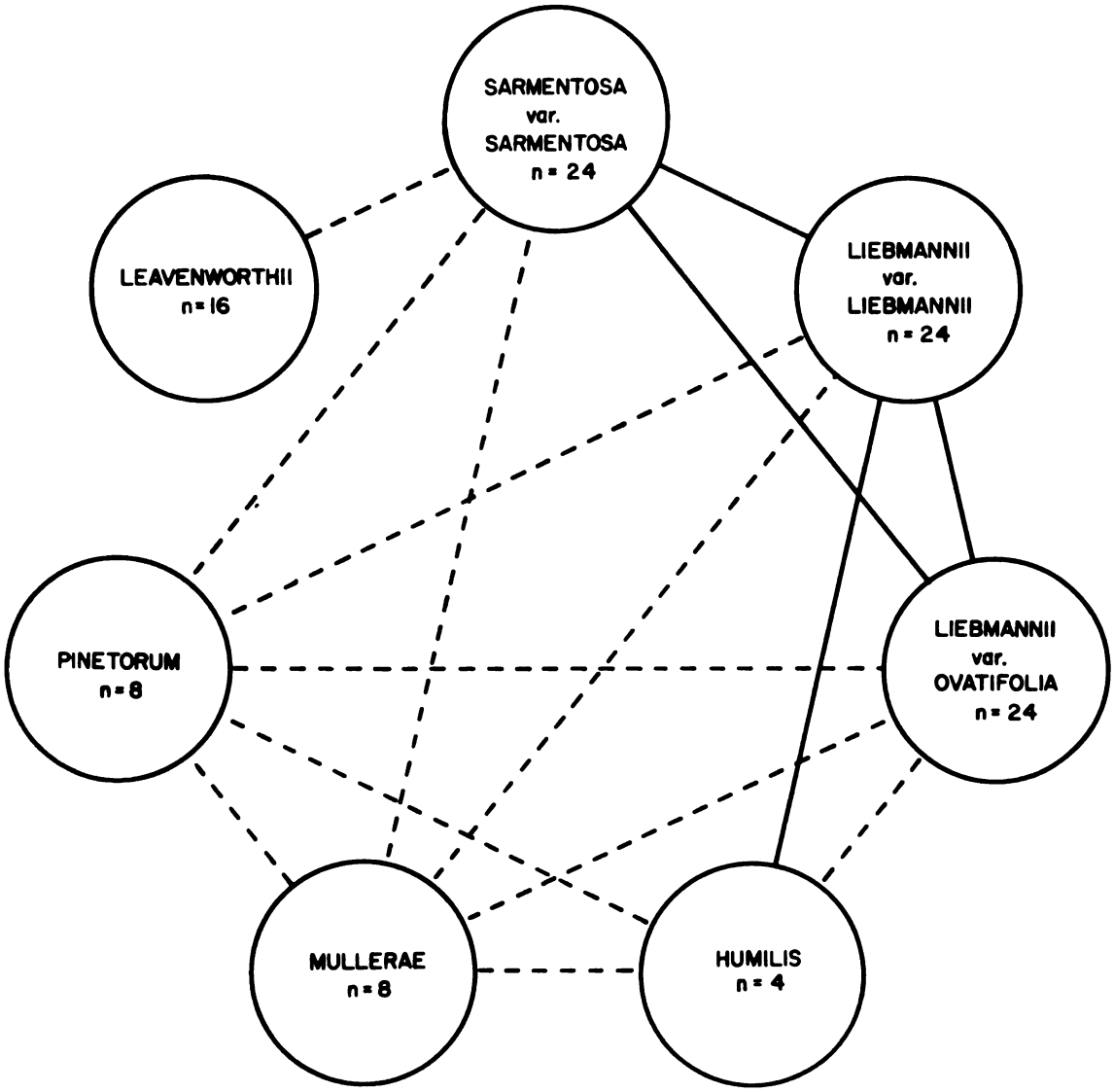
Three species of Sabazia, S. multiradiata, S. mullerae and S. pinetorum, possess a few morphological characters identical to those of Calea but differ in having a chromosome number of n = 8. Chromosome counts of Calea have been reported to be n = 9, n = 16, n = 18, and n = 32 by Turner et al. (1961; 1962), De Jong and Longpre (1963) and Powell and Turner (1963). From the present information, x = 16 and x = 9 appear to be the likely base numbers for the genus Calea.

Crossing Studies.

Five species of Sabazia were used in attempting experimental interspecific crosses under greenhouse conditions (Fig. 2). Likewise, infraspecific crosses involving two varieties of S. liebmannii were carried out.

Heads of Sabazia were found to be almost completely self-incompatible when florets from one head were selfed during early to late anthesis. Fertility, measured in terms of fruit set and germination, was almost negligible (about 0 to 1.5%). Consequently, it was not deemed necessary to emasculate the florets prior to artificial pollination.

Figure 2. Experimental crosses in Sabazia. Solid lines represent successful crosses, broken lines unsuccessful crosses.


SARMENTOSA
var.
SARMENTOSA
n = 24
LEAVENWORTHII
n = 16
LIEBMANNII
var.
LIEBMANNII
n = 24
PINETORUM
n = 8
LIEBMANNII
var.
OVATIFOLIA
n = 24
MULLERAE
n = 8
HUMILIS
n = 4

In many of the unsuccessful crosses, black achenes of normal appearance recovered from the parents were found to be empty or else contained aborted embryos. However, in some of the unsuccessful crosses the black achenes from the parent plants appeared to be superficially fertile in having plump and "succulent" embryos. This condition occurred in crosses of S. liebmannii var. ovatifolia X S. humilis and S. leavenworthii X S. sarmentosa. Seed from these crosses never germinated, however, even after being subjected to various periods of cold treatment. On the other hand, under comparable germination procedures, seed obtained from each of the parental species could be readily germinated.

Three interspecific crosses involving three species of Sabazia (including two varieties of S. liebmannii) were consistently successful, but in every case the F_1 hybrids proved to be sterile. Reciprocal intraspecific crosses were attempted with S. liebmannii var. ovatifolia in order to verify whether or not genetic isolation occurs between these two varieties. Hybrids from this cross were easily cultivated.

1. Interspecific Crosses

1. S. sarmentosa var. sarmentosa (n = 24) X S. liebmannii var. liebmannii (n = 24).

Pollen stainability of the former parent was 98.2% while that of the latter was 93.7%. The F_1 hybrid pollen

had stainability of 90.7%, somewhat lower than either parent. Cytogenetic examination of the pollen mother cells belonging to the F_1 hybrids showed the frequent occurrence of one or more trivalents and univalents. These interchange complexes were oriented in ring or zig-zag configurations. Chromosomal fragments were observed in various meiotic phases. These meiotic irregularities must be responsible, at least in part, for the sterility of the F_1 hybrids, resulting in the failure of seeds to germinate. Furthermore, although some difficulties in germination of F_1 hybrids are attributed to endosperm failure (Brock, 1956), studies by Brock (1955) on hyacinth showed that chromosomally unbalanced embryos had not been eliminated sixteen days after pollination. His later studies indicated that physiological as well as cytological factors affect not only the ability to undergo mitosis, but also the process of differentiation resulting in failure of the F_1 seed to germinate and in the cessation of early seedling growth. Leaf morphology of the F_1 hybrids was intermediate quantitatively as well as qualitatively.

2. S. liebmannii var. ovatifolia (n = 24) X S. sarmentosa var. sarmentosa (n = 24).

Pollen stainability for var. ovatifolia was 98.6% in contrast to 65% found in the F_1 hybrids. Meiotic irregularities in the pollen mother cells appeared to be as frequent

as in hybrids of Sabazia sarmentosa var sarmentosa X S. liebmannii var. liebmannii. The few achenes harvested from the F_1 hybrids failed to germinate. As in the previous cross, leaf characters in the F_1 hybrids were intermediate in size and shape. Moreover, leaf pubescence, which was largely attributed to var. ovatifolia, was more dense than var. sarmentosa but was half as dense as var. ovatifolia.

3. S. humilis (n = 4) X S. liebmannii var. liebmannii (n = 24).

Pollen stainability in S. humilis ranged from 89.7% to 93%, unlike the F_1 hybrids with only 80% stainability. The pollen mother cells of the F_1 hybrids revealed numerous fragments and clumping of chromosomes. Vegetative morphology of the F_1 hybrids resembled that of S. liebmannii var. liebmannii rather than being intermediate in characters as in the previous crosses. This one-sided phenotype may be attributed to the chromosomal dominance of S. liebmannii var. liebmannii.

2. Intraspecific Crosses

1. S. liebmannii var. ovatifolia X S. liebmannii var. liebmannii.

Pollen stainability of the F_1 hybrid was 97.6%. When compared to the parents, var. ovatifolia with 98.6% and var. liebmannii with 93.7% pollen stainability, there appears

to be little difference in pollen quality between the hybrids and the parental taxa. During diakenesis no meiotic irregularities were observed except for one small chromosome fragment which was consistently present. The F_1 hybrids were intermediate between the two parental varieties in leaf shape, leaf margin and density of stem and leaf pubescence.

Discussion. From attempts to make crosses in thirteen directions within Sabazia, only three were successful in establishing F_1 hybrids. Two of the successful crosses involving S. sarmentosa and two varieties of S. liebmannii were homoploid (n = 24). The remaining was a heteroploid cross between S. humilis (n = 4) and S. liebmannii var. liebmannii (n = 24). Hybrids of all the interspecific crosses displayed irregular meiotic activity, vegetative characters intermediate between the parents (with the exception of the S. humilis X S. liebmannii hybrid), and generally a lower percentage of pollen stainability than either parent. Despite the high degree of reciprocal crossability, all interspecific and intraspecific hybrids were sterile. Although crossing between these few species and varieties is not impossible, sterility of the F_1 hybrids appears to prohibit any gene flow between these taxa. It seems probable that evolution at the diploid and polyploid level in Sabazia has resulted in genic and chromosomal changes which have led to phenetic diversification and to genetic isolation between populations.

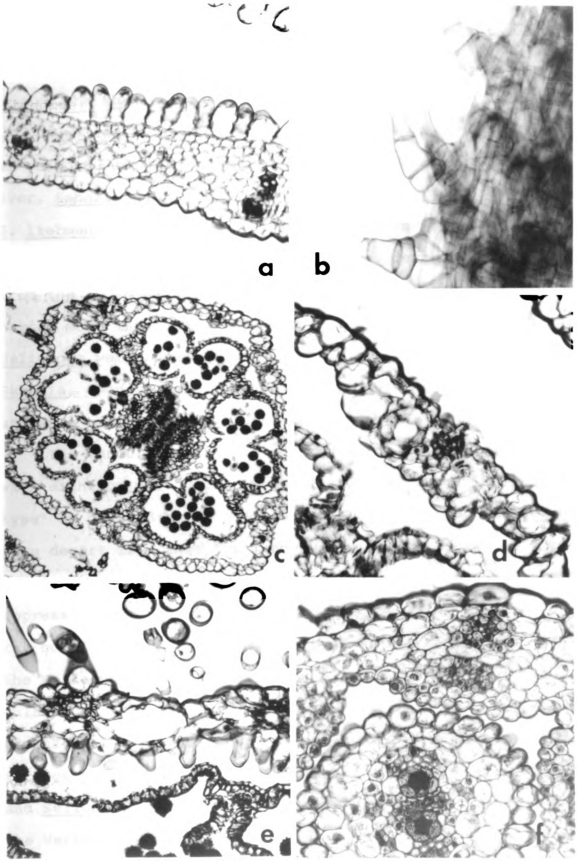
ANATOMY

Ray Corolla.

There is little histological variation in the ray corolla of most Sabazia species. The ligules are six to eight cells thick at their broadest point. The adaxial epidermal cells are papillate or "nipple-like" (Plate 1a). However, S. multiradiata lacks these papillate, epidermal cells and is characterized instead by rectangular cells which are about three times larger than those of the abaxial epidermis. The rays of S. liebmannii var. liebmannii have large bulliform cells interspersed at random in the adaxial epidermis. In S. leavenworthii, Selloa and Galinsoga, the ligule tissue appears as a series of "mounds" near the abaxial surface with a vascular bundle embedded in each of these mounds.

Individual secretory canals are usually associated with vascular bundles oriented near the abaxial side of the ligule. Near the base of the ray tube, the secretory canals are usually in pairs, one on each side of vascular bundle. Sabazia pinetorum differs in lacking secretory canals. The vascular bundles of S. acoma are distinct from all other species in being situated in the middle of the ligule tissue. Sabazia multiradiata deviates from other

Plate 1. Ray and disc corolla transections of *Sabazia* and *Calea*. a. *S. trianae* with papillate adaxial epidermal cells, X 296. b. *S. liebmannii* var. *liebmannii* showing several-celled trichomes on tube of disc floret, X 226. c. Transection of a disc floret of *S. sarmentosa* var. *sarmentosa* with the corolla, connate anthers and stigmatic branches, X 113. d. Part of a disc corolla of *S. sarmentosa* var. *sarmentosa* showing the vascular bundle between two secretory canals, X 417. e. Disc corolla of *C. palmeri* showing large lacunae, X 227. f. Inner filament vascular bundle of *S. sarmentosa* var. *sarmentosa* adjacent to disc corolla vascular bundle just above their point of fusion, X 296.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species of Sabazia in having the xylem of the collateral bundle located toward the adaxial epidermis rather than toward the abaxial side.

The ligule tissue within the confines of the epidermis is composed mostly of compact parenchymatous cells. However, Sabazia humilis, S. sarmentosa var. sarmentosa, and S. liebmannii are unusual in possessing many air lacunae throughout the ligule. Sabazia mullerae deviates somewhat from the above pattern in exhibiting fewer lacunae and in having more irregular cell walls. The ligules of Selloa and Galinsoga were found to be anatomically similar to those of Sabazia, even though secretory canals were less frequent and were usually not associated with vascular bundles.

The vascularization in the ray corolla of Sabazia, with eight or more veins in the ligule is of the "Heliantheae type" as defined by Koch (1930). Sabazia, Selloa and Galinsoga depart from this type, however, in lacking two or three prominent large veins. Koch contended that such veins are appressed calyx bundles, fused to the abaxial surface of ray corollas, and that they are typical for most genera of the Heliantheae. In these three genera, however, the vascular bundles are embedded in compact parenchyma. The appressed calyx bundles are not present. This anatomical difference provides one line of evidence suggesting that Sabazia and Selloa belong in the subtribe Galinsogineae rather than the Verbesininae.

Disc Corolla.

In most species of Sabazia and related genera, there are uniseriate trichomes of one to three cells in length on the external surface of the corolla lobe. Sabazia liebmannii var. liebmannii differs in possessing longer trichomes of three to five cells. Tricarpha purpusii is devoid of such hairs on the lobes. The inner surface of the lobes of these genera is characterized by numerous elongate, papillate cells which range from 12.7 to 36.4 microns in length; the papillate cells of S. humilis and S. liebmannii var. liebmannii, however, are unusually long, attaining a length of 63.7 and 72.8 microns respectively.

The corolla lobes in Sabazia multiradiata, S. mullerae, S. sarmentosa var. sarmentosa, and S. liebmannii var. liebmannii are five to six cells wide. The outer, cutinized epidermal cells, and the inner papillose epidermal cells are three to four times larger than the cells interior to them. The remaining species of Sabazia, as well as those of related genera, are characterized by corolla lobes two to four cells thick. Sabazia trianae is distinct in having outer epidermal cells that are two to six times larger than the inner second and third layers. Furthermore, the inner epidermal papillae are five to twenty times larger than the cells of the central tissue.

In each of the five lobes there are two lateral vas-

cular bundles. A secretory canal is associated, externally or laterally, with each bundle and averages about 36 microns in diameter (Plate 1d). The secretory canals of Sabazia pinetorum, however, are much smaller, ranging from 10.9 to 18.2 microns in diameter including the epithelial cells. The genus Selloa deviates from the above pattern in usually having only one secretory canal associated with each vascular bundle.

In light of Carlquist's 1961 summation of vascular evolution in the Compositae, nearly all species of Sabazia and related genera appear to be fairly advanced in their disc corolla venation patterns. The florets are characterized by simplified venation typical of most tribes. Five vascular bundles, which represent a fusion of ten adjacent lateral vascular bundles in the primitive corolla, arise from the base of the corolla. The five median vascular bundles of the corolla have been lost. At the sinus of each corolla lobe the individual bundle bifurcates, with a vein extending into the lobe along the margin. In all species studied, the two veins in each lobe meet and fuse at the lobe apex.

In all of the taxa studied the corolla is two cells thick commencing just below the lobe sinuses and extending downward to a point where the filaments are adnate to the corolla. This condition is typical of the Heliantheae. A secretory canal is adjacent to, and on either side of, each

of the five vascular bundles which are opposite the connective of the stamens. These canals progressively diminish in size toward the point where the filaments depart from the corolla. Galinsoga is distinct in having numerous vascular bundles, each vein with four to eight xylem cells rather than one to four, which are typical of the other taxa studied. Moreover, the secretory canals are not necessarily associated with a vascular bundle, and there appears to be more variation in their size. Calea palmeri is unique in possessing huge air lacunae (four times the size of the secretory canals) near the secretory canals (Plate 1e).

At and below the point of filament adnation, the corolla tube in all species studied is five to seven cells thick, and no secretory canals are present. Each filament bundle fuses with a lateral corolla bundle (Plate 1f). In S. liebmannii, S. sarmentosa, and S. leavenworthii, however, one may find eight vascular bundles in corollas at the extreme periphery of the head, while the inner florets typically possess five bundles. Calea palmeri is similar in this respect, but differs in having seven instead of eight vascular bundles in the peripheral disc florets.

The exterior of the corolla tubes of all species is characteristically covered by uniseriate tapered trichomes which are two to six cells in length (Plate 1b). The extent, density and length of the trichomes varies from individual to individual as well as interspecifically. Galinsoga

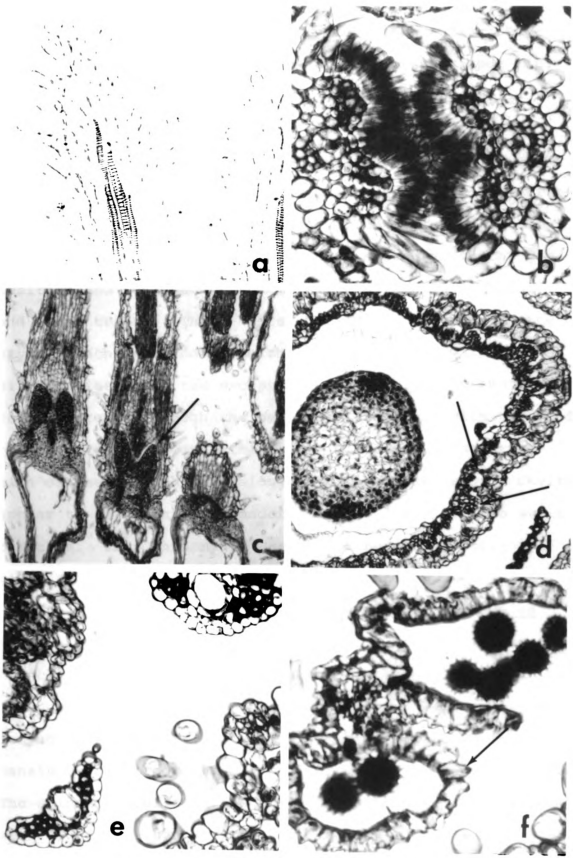
parviflora is the only species whose trichomes extend continuously from the base of the corolla to the apex of the lobes. The six- to eight-celled tapered trichomes of Selloa plantaginea are the longest of any species.

Style.

The styles of Sabazia and related genera differ in minor respects. The stigmatic branch apices, in the majority of the species, are acute at early anthesis (Plate 2a). However, Sabazia humilis, S. pinetorum and Selloa plantaginea tend to have a subulate or deltoid stylar apex. During late anthesis, the stigmatic branches are recurved and tend to project out above the corolla lobes.

Elongate collecting hairs completely or partially cover the external surfaces of the stigmatic branches and are typically Helianthoid in structure and distribution. They extend from just below the apex, where they are more dense, to one-half to three-quarters the distance from the point where the branches diverge. Other species of Sabazia and allied genera show a departure from the above generalized type. In Galinsoga parviflora the collecting hairs are largely restricted to about the upper one-third of the style branch. In contrast, the collecting hairs of Sabazia leavenworthii and S. liebmannii completely cover the stigmatic branch.

Plate 2. Styles, nectaries, achene walls and pales of *Sabazia* and anthers of *Calea*. a. Whole mount of *S. leavenworthii* style branch apex, X 234. b. *C. palmeri* style transection showing stigmatic hairs on either side of cavity, dark stigmatoid tissue abaxial to secretory canal and vascular bundle outside secretory canal, X 327. c. Longitudinal section of *S. liebmannii* var. *ovatifolia* showing nectary (indicated by an arrow) surrounding style base, X 50. d. *S. humilis* achene wall transection showing "mounds" alternated by "pillars" of tissue as indicated by arrows, X 100. e. Dark fibrous tissue and secretory canal of pale transection of *S. sarmentosa* var. *triangularis*, X 313. f. Transection showing ribs in anther wall of *C. palmeri* as indicated by an arrow, X 688.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The stigmatic hairs generally cover the entire inner surface of the style branches except near the extreme tip. In Sabazia humilis, S. pinetorum, and S. leavenworthii, however, each band of stigmatic hairs may be divided for a short distance downward before fusing into one continuous band, which extends to the style branch base. This restriction of stigmatic hairs into marginal bands is regarded by Cronquist (1955) as being an advanced character in the Compositae, and is found in the majority of the Heliantheae and other tribes. These hairs continue to run beneath the style-branch junction diminishing shortly afterwards. In all Sabazias, with the exception of S. humilis, a short cavity extends through the center of the style with two bands of stigmatic hairs on either side (Plate 2b). The extension of these trichomes, along with the presence of a cavity, appear to represent a secondary partial fusion of the style branches. This phenomenon was also observed by Carlquist (1957) in his study of Fitchia (Heliantheae).

In all species studied, with the exception of Calea palmeri, one secretory canal is found in each stigmatic branch (Plate 2b). Both canals are continuous downward through the style to a point where the style enlarges, becoming three to four cells thick, whereupon the secretory canals become progressively smaller and eventually disappear. The epidermal cells of the style near the base are generally more elongated than are those of the inner cells. In Calea

palmeri each secretory canal divides to form two canals about one-fifth to one-fourth the distance from the stylar apex. Consequently, a total of four secretory canals continue to extend downward from the apex, ultimately becoming smaller and disappearing at a point about one-half to three-quarters the length of the style.

The two collateral bundles, each of which commences just before the apex of the stigmatic branch, descend parallel to the base of the style. At that point, each stylar vascular bundle joins an achene bundle. In most species studied, the vascular bundles are parallel and external to the secretory canals, with two bands of stigmatoid tissue internal to, but parallel with the secretory canals. Calea palmeri is distinctive in possessing four additional vascular bundles in the style at a level corresponding to where the four secretory canals appear.

In three species, Sabazia mullerae, S. trianae, and S. pinetorum, collenchyma was observed in the outer epidermal layer of the style. This tissue occurred in about one-third to three-quarters the length from the stylar apex. Nectaries were also found surrounding the base of the styles in all species (Plate 2c) except Sabazia multiradiata and Calea palmeri.

Achene and Pappus.

A single vascular bundle from the receptacle extends

into the base of the disc achene. This condition is common in most members of the Compositae according to Carlquist (1961). Generally, this bundle gives rise to five outer bundles extending upward in the achene wall. In almost half of the species of Sabazia this number varies from six to ten vascular bundles, depending upon the species. Sabazia liebmannii var. liebmannii, S. liebmannii var. ovatifolia, and Calea palmeri, with ten outer vascular bundles in the achene wall, are regarded as representing a more primitive condition. Observations of achenial anatomy in Galinsoga agree with those of Majdecka-Zdziarska (1929). Selloa and Tricarpha exhibit the common condition of five vascular bundles in the ovary wall. The vascular bundles of all taxa studied include one to three tracheids.

Trichomes, when present on disc or ray achenes, are of the "zwillingshaar" type, a biseriate non-glandular trichome typical of many Compositae. The tips of the two apical cells usually do not terminate at the same point. The length of these trichomes generally ranges from 30 to 173 microns. Aside from this, the only major variation occurs in Sabazia mullerae, S. leavenworthii, S. liebmannii var. liebmannii, and Calea palmeri, in which the biseriate trichomes are also two cells in height. The basal cells of the trichome are quite small, about one-sixth or one-seventh of the total trichome length. The achenes of Selloa obtusata are unique in possessing uniseriate trichomes which are three cells

in height. A collar or corona of callous cells frequently appears on the summit of the ray achenes in all of the genera studied. It is composed of one layer of rectangular cells, varying in height from about 15 microns in Galinsoga to 55 microns in Sabazia.

The anatomical structure of the achene wall in Sabazia resembles very closely that of Tithonia rotundifolia (Carlquist, 1957) and Helianthus annuus (Hanausek, 1902). It is made up of an epidermal layer beneath which is a layer of larger cells, the hypodermis; beneath the hypodermis is a layer of smaller sub-hypodermal cells two to four cells in thickness, in which the vascular bundles are embedded. Internal to these cells is the parenchymatous ground tissue, which may be two to five cells in thickness depending upon the species. The cells of the ground tissue are usually larger than the sub-hypodermal cells.

As the pericarp matures, the sub-hypodermis becomes sclerified, forming a series of "pyramids" or "mounds" of fibers two to three cells high and four to five cells wide at the base. These mounds are usually separated by "pillars" of tissue which connect the sub-hypodermis with the hypodermis (Plate 2d). As achene maturation progresses, the sclerified sub-hypodermal layers shrink away from the hypodermis leaving air chambers. Consequently, this developmental pattern results in an alternation of a pillar with a mound within each air chamber. In some species such as Sabazia

multiradiata and S. mullerae, the ground tissue is made up of two layers of collenchyma rather than of parenchyma. Galinsoga differs from the other genera in lacking air chambers in the mature pericarp, although the sub-hypodermis is composed of two to three sclerified cells.

Transections of pappus scales or awns of the various species studied show relatively little cellular differentiation. The pappus in cross section may be triangular, round, or rectangular. In S. mullerae the awns are characterized by all of the above shapes. Other species (S. trianae, S. pinetorum, Selloa obtusata and Calea palmeri) show a marked departure from the other types in possessing fusiform awns. The scales or awns are generally two to four cells in thickness at their widest part. As in Fitchia (Carlquist, 1957), sclerification may begin in the epidermis and proceed centripetally to the inner sub-epidermal layers. The degree of sclerification, which varies among the species, is usually initiated at the base of the scale or awn and progresses distally as the achene matures.

Stamens.

The stamens of Sabazia, Selloa, Tricarpha and allied genera are basically similar in their histology. The fibrous layer of the anther wall in surface view is classified as "polarized" tissue, according to Dormer (1962).

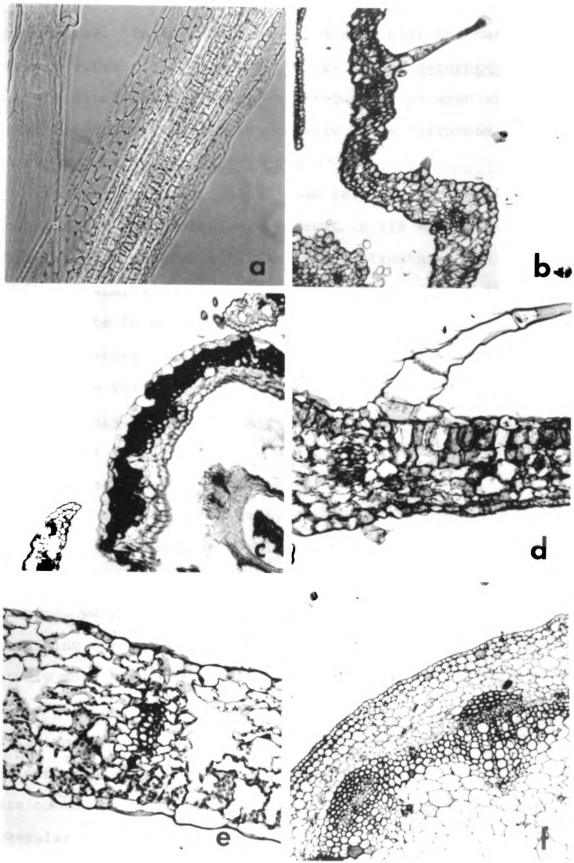
The anticlinal walls of the above cells possess one to few internal ribs, which are perpendicular to the anther surface (Plate 2f). This thickening extends throughout the cell from one periclinal wall to another. The "polarized" condition appears to be common for the Heliantheae as a whole.

In only one instance is there any deviation from the typical histological pattern. Tricarpha purpusii is distinctive in having anther tissue only three to four cells wide on either side of the connective tissue, in contrast to a wider area of six to ten cells in the other genera (Plate 3a).

Involucre and Pales.

Comparative histological studies of the phyllaries and pales of the genera in question show few major differences; their structure is fundamentally the same for most species. Transections from the upper half of the outer phyllaries reveal compact, isodiametric, parenchymatous cells internal to the epidermis. However, Selloa obtusata was characterized by spongy mesophyll tissue with huge (but few) air lacunae. The outer phyllaries vary from three to six cells in thickness, although those of Galinsoga parviflora and Sabazia multiradiata are typically seven and nine cells thick, respectively. The epidermis may or may not possess a cuticle on the upper half of the phyllary, depending upon

Plate 3. Anther, phyllary and leaf features of *Tricarpha* and *Sabazia*. a. *T. purpusii* whole mount of anther showing cellular width on either side of connective tissue, X 258. b. Phyllary transection of *S. sarmentosa* var. *triangularis* showing glandular trichomes and abaxial secretory canal adjacent to vascular bundle, X 95. c. Outer phyllary transection of *S. acoma* showing dark sclerotic tissue towards adaxial side, X 70. d. *S. leavenworthii* leaf transection showing a palisade layer (top is adaxial side), X 200. e. *S. liebmannii* var. *liebmannii* leaf transection showing no distinct palisade layer, X 206. f. Stem transection of *S. sarmentosa* var. *sarmentosa*, X 74.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the species. In contrast, the epidermis near the base usually shows a cuticle. In Sabazia humilis and S. sarmentosa uniseriate glandular trichomes may frequently be seen along the outer epidermis (Plate 3b); likewise these trichomes are fairly common in Selloa obtusata.

Secretory canals (and in some cases secretory cavities) in the outer phyllaries were present in all species studied. These generally large and conspicuous structures are located on the adaxial side of the vascular bundle. Calea and Galinsoga deviate from the above pattern in possessing relatively small secretory canals. The number of canals varies from one to five for most taxa, but there may be as many as seven in Selloa plantaginea, or eleven in Sabazia acoma. Selloa obtusata is unique in having a secretory canal on the abaxial side of the midvein as well as on the adaxial side. The collateral bundles are usually ensheathed by parenchymatous cells; sclerenchymatous bundle sheaths are absent.

In most species diffused sclerids, or patches of sclerenchyma, were noted in the outer phyllaries. Sclerification involving one to three layers of mesophyll becomes progressively more pronounced near the base of all phyllaries (Plate 3c). The inner phyllaries, in contrast to the outer, are relatively longer and narrower, with an earlier and more extensive development of sclerenchyma. Secretory canals are commonly present and may or may not be associated with vascular bundles.

The pales in all of the species studied lack vascular bundles. They are generally shorter in length and are only one to three cells thick in comparison to the inner phyllaries which have three to six cell layers. The presence of fibrous cells in the pales is the rule rather than the exception (Plate 2e). Secretory canals are fewer in number (one to three) than in the phyllaries; they are totally absent in the pales of Sabazia humilis. In S. mullerae, S. pinetorum, S. sarmentosa, and S. leavenworthii, the pales toward the base become horseshoe-shaped in transection, partially enclosing the ovaries. Selloa plantaginea is distinguished from all taxa (including S. obtusata) in having pales which are circular in transection. The center is occupied by a secretory canal which is surrounded by one or two layers of parenchyma followed by one or two layers of sclerenchyma.

Leaf.

Most species of Sabazia, Selloa, Tricarpha and related genera are characterized by one of two basic patterns in leaf anatomy. The first group includes Sabazia humilis, S. liebmannii var. liebmannii and var. ovatifolia. This group is characterized by having little or no differentiation of a palisade layer (Plate 3e). The mesophyll is about six or seven cells in thickness and contains abundant chloroplasts throughout the tissue except for the parenchymatous

sheath surrounding the collateral vascular bundles. The spongy mesophyll is composed of loosely arranged cells with many air lacunae. The epidermal or subepidermal walls become thickened in the curved region above or below the midvein and the prominent secondary veins. Stomata are restricted to the abaxial epidermal layer which is lightly cutinized. The leaves of Selloa plantaginea deviate from the above description in possessing prominent secretory canals associated adaxially with the vascular bundles. Moreover, S. plantaginea is the only species studied which possesses a pair of either adaxial or abaxial secretory canals with larger veins.

The second group, which includes Sabazia multiradiata, S. mullerae, S. acoma, and S. leavenworthii, displays a distinct palisade layer (Plate 3d). The cells are somewhat rectangular and are less isodiametric; generally they have more chloroplasts than are in the remaining mesophyll tissue which is compact with very few (if any) air lacunae. Secretory canals are present and are associated adaxially with the vascular bundles, although in Tricarpha purpusii they may be situated abaxially as well. With the exception of Sabazia trianae, the species belonging to this group do not have a sclerenchymatous bundle sheath around the midvein nor around the larger secondary veins. However, in Sabazia liebmannii thickened epidermal and subepidermal tissue may develop on either side of the larger veins.

Sabazia pinetorum is somewhat anomalous in its leaf anatomy since it does not conform exactly to the description of either of the two groups above. Histologically it belongs to the first group despite the fact it has one layer of palisade cells slightly rectangular in shape.

Stem.

The stem anatomy in Sabazia is typical for an herbaceous dicot. The young stem is composed of eleven to thirteen collateral bundles, each with a bundle cap of protophloem fibers. The bundles lie in a ring toward the periphery of the stem and adjacent to the endodermis. The endodermis consists of a continuous layer one cell thick of cells usually larger than the remaining cortical cells; occasionally casparian strips may be seen. The outer cortex may or may not be circumscribed by a layer of collenchyma. Secretory canals are typically situated between the primary vascular bundles or opposite the interfasicular region adjacent to the endodermis within the cortex. This location appears to be characteristic of most composites with secretory canals in the cortex, as noted by Metcalfe and Chalk (1950). The epidermal cell walls become thickened with age, despite the absence of cortical collenchyma in some species. The pith occupies a relatively large area of the stem in contrast to the vascular and cortical tissue.

The thin-walled parenchymatous cells are four to five times the size of the cortical cells. An exception to this condition is found in Sabazia liebmannii var. liebmannii and var. ovatifolia, in which the pith cells show slight sclerification in older stems.

Interfasicular development of vascular tissue or fibers is common in the older stems of most species of Sabazia, as illustrated in Plate 3f. However, S. acoma, S. leavenworthii and S. liebmannii differ in lacking the above tissue development. The bundles remain separate, as evidenced by the presence of medullary rays, although these rays may be reduced or obliterated as the bundles expand or "fan out", largely through anticlinal divisions. This latter condition is exemplified in S. liebmannii and S. trianae. Sabazia sarmentosa var. triangularis exhibits considerable diversity in stem structure owing to its two to four cortical collenchyma layers, unusually large vessels, and relatively more abundant secretory canals in contrast to most other Sabazia species.

Calea palmeri resembles Sabazia fairly closely in stem anatomy, but differs in the following three ways. First, sixteen vascular bundles are present as opposed to the eleven to thirteen bundles in Sabazia. Second, Calea palmeri has three layers of cortical collenchyma while Sabazia is characterized by one layer of collenchyma. Finally, there is more extensive secondary phloem development in Calea

palmeri; the phloem of Calea is composed of six to seven cell layers in contrast to Sabazia phloem of two to four cell layers. Tricarpha purpusii is basically similar to Sabazia in stem anatomy, but is distinguished in possessing the largest secretory canals observed in all of the taxa studied, in addition to having fourteen vascular bundles. Selloa plantaginea and S. obtusata differ from members of the other genera in having a ring of protophloem fibers which connects all vascular bundles.

Stem anatomy is essentially the same for all Sabazia species notwithstanding the minor differences noted above. There are outstanding differences, however, between Sabazia and allied genera. The stem anatomy of Selloa is especially distinctive and provides one line of evidence supporting the transfer of Sabazia obtusata to Selloa.

POLLEN MORPHOLOGY

With respect to pollen grains, the observed genera are of the "Helianthus type", as expressed by Stix (1960). The spores are tritreme and zonocoloporate, and are generally oblate-spheroidal in shape. The colpi are long and narrow, with thin margins, which become acuminate at both ends and exhibit a smooth membrane (Plate 4a). The ora are also longitudinally elongate with thin margins and acuminate ends. The tegillate-baculate sexine (tectum) is covered by evenly-spaced spines. The length and shape of the spines have been observed to be reliable taxonomic characters for some species. Spine length ranges from 3.0 microns in Sabazia liebmannii var. liebmannii to 6.9 microns in Tridax balbisioides (Table 3). A correlation between spine length and pollen diameter was established in Sabazia and Selloa. With the exception of Sabazia liebmannii var. michoacana and S. sarmentosa var. sarmentosa, it was noted that the greater the mean diameter of spores of a given species, the longer were the spines (Table 4).

Although ranges in pollen grain size overlap in some species of Sabazia, size differences were noted initially between certain species. Therefore, an attempt was made to determine whether variation in size was correlated with variation in chromosome number. The results indicate that

Plate 4. Pollen grain whole mounts of Sabazia, Selloa, Calea and Galinsoga. a. Surface view of Sabazia liebmannii var. ovatifolia showing a long narrow colpus and an ora with acuminate ends and thin margins, ca. X 1160. b. Spines of Sabazia humilis, ca. X 1280. c. Spines of G. parviflora, ca. X 1449. d. Spines of Sabazia mullerae, ca. X 1116. e. Equatorial view of Sabazia mullerae, ca. X 1116. f. Spines of Sabazia leavenworthii, ca. X 1261. g. Spines of Sabazia liebmannii var. liebmannii, ca. X 1225. h. Large and long lacunae in spines of C. palmeri (equatorial view), ca. X 1330. i. Small lacunae scattered throughout spines of Selloa plantaginea (equatorial view), ca. X 1165.

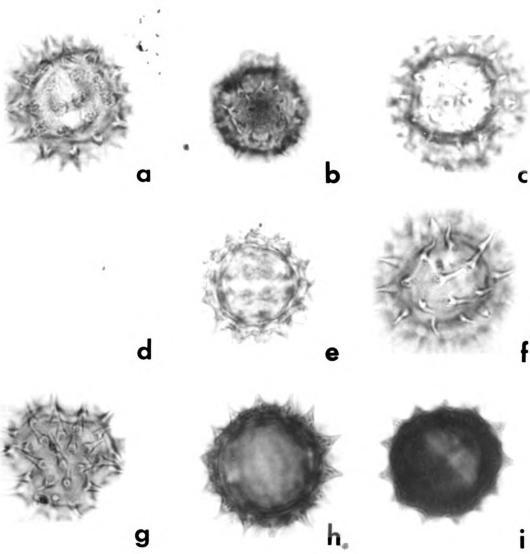
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Table 3. Pollen grain measurements of selected Heliantheae (all measurements are in microns).

taxon	diameter range[a]	mean diameter	spine range[b]	mean spine length
Sabazia multiradiata	18.0 - 22.1	20.0		
S. mullerae	20.2 - 24.6	22.4	2.5 - 3.8	3.6
S. pinetorum	20.8 - 26.5	22.3	3.2 - 3.8	3.3
S. leavenworthii	21.4 - 25.2	23.8	3.2 - 5.0	4.2
S. sarmentosa var. sarmentosa	22.7 - 28.4	25.5	3.2 - 5.0	4.4
S. sarmentosa var. triangularis	20.8 - 28.4	24.9	3.8 - 5.7	4.5
S. sarmentosa var. lancifolia	19.2 - 21.6	20.4		
S. liebmannii var. liebmannii	22.1 - 27.7	24.4	3.2 - 5.7	4.4
S. liebmannii var. ovatifolia	22.1 - 27.7	25.0	3.8 - 5.7	4.5
S. liebmannii var. michoacana	20.2 - 28.8	24.0	2.5 - 4.4	3.5
S. humilis	18.7 - 24.0	21.1	2.5 - 3.2	3.0
Selloa plantaginea	24.6 - 28.4	26.6	3.8 - 6.3	4.5
S. obtusata	22.1 - 25.2	23.2	3.2 - 4.4	3.8
Tricarpha purpusii	18.9 - 22.7	21.1	3.2 - 5.0	4.2
Calea palmeri	19.5 - 23.9	21.8	3.2 - 4.4	3.7
Galinsoga hispida	17.1 - 24.6	20.7	2.5 - 3.8	3.2
Tridax balbisioides	21.4 - 28.9	24.9	3.8 - 7.0	5.4
T. trilobata	22.7 - 25.2	23.9	3.8 - 5.7	4.8
Verbesina liebmannii	18.3 - 20.8	19.2	3.2 - 3.8	3.5

(a) Average range in diameters of single grains within any species was 4.9 microns. Standard deviation of individual pollen grain diameters was 1.08 microns, and average standard error of each species mean was 0.08 microns.

(b) Corresponding figures for spine length were: average range -- 1.50 microns; standard deviation of spine length of individual pollen grains -- 0.33 microns; average standard error of each species mean -- 0.024 microns.

Table 4. Relationship of pollen grain size to spine length in *Sabazia* and *Selloa* (All measurements are in microns).

taxon	mean diameter	mean spine length
Sabazia humilis	21.1	3.0
S. pinetorum	22.3	3.3
S. mullerae	22.4	3.6
S. leavenworthii	23.8	4.2
S. liebmannii var. *michoacana*	24.0	3.5
S. liebmannii var. *liebmannii*	24.4	4.4
S. sarmentosa var. *triangularis*	24.9	4.5
S. liebmannii var. *ovatifolia*	25.0	4.5
S. sarmentosa var. *sarmentosa*	25.5	4.4
Selloa obtusata	23.2	3.8
S. plantaginea	26.6	4.5

there is a correlation between increasing spore diameter and chromosome number (Table 5). Sabazia humilis, with n = 4, has a diameter range of 18.7 to 24.0 microns, and a mean diameter of 21.1 microns. Sabazia pinetorum and S. mullerae, with n = 8, fall within the range of 22.2 to 26.5 microns and have progressively higher mean diameters of 22.2 and 22.4 respectively. Sabazia leavenworthii is the only species with n = 16 and has a range of 21.4 to 25.2 microns, with a mean diameter of 23.8 microns. The last group, comprising two species, is characterized by n = 24. They possess the largest mean diameter of all Sabazia species (24.4-25.5 microns) and exhibit a range of 22.1-28.4 microns. Based on the above data, it can be predicated that Sabazia sarmentosa var. triangularis, having a mean spore diameter of 24.9 microns and not cytologically investigated, would possess a chromosome complement of n = 24.

Despite the fact that pollen grain size ranges overlap between ploidy levels, statistical analysis demonstrated that there are significant differences between two sample means. All populations representing one level of ploidy, were considered as one sample mean. In employing the "t distribution" for a two-tailed test, it was found that the difference between the two means (two populations each with different chromosome numbers) was significantly different at the 0.5% level.

Differences in spore morphology were observed at the

Table 5. Relationship of pollen grain size to chromosome number in Sabazia (all measurements are in microns).

taxon	n number	diameter range	mean diameter
S. humilis	4	18.7 - 24.0	21.1
S. multiradiata	8	18.0 - 22.1	20.0
S. pinetorum	8	20.8 - 26.6	22.3
S. mullerae	8	20.2 - 24.6	22.4
S. leavenworthii	16	21.4 - 25.2	23.8
S. liebmannii var. liebmannii	24	22.1 - 27.7	24.4
S. liebmannii var. ovatifolia	24	22.1 - 27.7	25.0
S. sarmentosa var. sarmentosa	24	22.7 - 28.4	25.5

generic level, and in some cases at the specific and subspecific levels. The pollen grains of most Galinsogas, for example, are distinctly larger with more numerous spines and possess a thicker-walled sporoderm than in Sabazia (Plate 4b and 4c).

Pollen morphology at the infraspecific level appears to be correlated in Sabazia sarmentosa var. sarmentosa and var. triangularis. The pollen of these varieties is similar

in the sporoderm, spine density, and spine length. Likewise, the identical grain size and spine length of S. liebmannii var. ovatifolia and var. michoacana substantiate the position of these taxa as varieties. However, var. michoacana is distinguished from the other varieties in having shorter spines.

Sabazia mullerae possesses very distinctive spines which are unlike any other Sabazia species. The spines show a close correspondence to Verbesina liebmannii in that they are more bulbous at the base than are the other species of Sabazia (Plate 4d and 4e). Sabazia leavenworthii is remarkable in that it is the only Sabazia species possessing crooked or undulating spines similar to those of Tridax balbisioides (Plate 4f). The former species, which appears to be closely related to Sabazia liebmannii (Plate 4g), has larger and fewer spines in a given area than does S. liebmannii.

As in Fitchia, Helianthus, and other members of the Heliantheae (Carlquist, 1957), "striae" or lacunae are exhibited in the pollen exine of Sabazia and related genera. These lacunae, or unstained areas, are restricted primarily to the spine base and are very infrequent in interspinal areas. Differences in size, number, and arrangement of the lacunae were observed in Fitchia and Helianthus by Carlquist. I have observed this variation also in genera allied to Sabazia. For example, the pollen grains of Calea palmeri

possess relatively larger lacunae, which extend higher within the spines than in Sabazia (Plate 4h). Selloa plantaginea is characterized by numerous small lacunae which are scattered throughout the entire spine (Plate 4i). On the other hand, Selloa obtusata has lacunae of the same type as in Calea palmeri. In equatorial view, Tridax trilobata exhibits a tapered portion of the ectosexine projecting two-thirds to three-quarters inside the length of the spine, which is unlike any of the other genera studied.

MORPHOLOGY OF SABAZIA

HABIT. Two species of Sabazia, S. humilis and S. microspermoides, are annuals; all the other species are perennials. Under greenhouse culture, the perennials came into flower as rapidly as the annuals. In culture S. humilis developed into a profusely branching plant with numerous small heads in contrast to plants collected in the field with solitary or few branches having larger and fewer heads. The plants range in habit from pendent to prostrate or trailing in some forms of S. sarmentosa to decumbent, ascending or erect in most other species. Adventitious roots are produced along the upper nodes only in S. sarmentosa var. sarmentosa and var. triangularis. The stems may be smooth or grooved and striate. Stem color is generally green to reddish-purple.

ROOTS. The majority of Sabazia species possess a slender horizontal or oblique rootstock with branching fibrous roots. Sabazia liebmannii has a similar root system but differs significantly in having a pronounced lignescent and a very stout rootstock. Sabazia microspermoides and S. sarmentosa lack any form of a caudex or rootstock, exhibiting only fibrous roots. Sabazia humilis and S. acoma are unique in being the only species with slender tap roots.

LEAVES. Despite some infraspecific variability in leaf characters, leaf morphology in Sabazia has been very useful in distinguishing species and varieties. Gradations in leaf shape range from ovate, elliptic, broadly lanceolate to linear-lanceolate. The margins vary from entire, remotely dentate to coarsely serrate. Leaf texture is typically herbaceous with the exception of subcoriaceous leaves in S. liebmannii var. hintonii. Reticulate venation arising from three primary costa near the leaf base is generally the rule. The secondary and tertiary veins of the leaf are weak and inconspicuous, although S. liebmannii var. michoacana is readily recognized by its very prominent reticulate secondary venation on the lower leaf surface.

PUBESCENCE. The stems, peduncles and leaves vary in having a sparsely pilose to densely strigose pubescence; rarely are they glabrous. The stems, peduncles and outer phyllaries often possess dark-purplish, capitate glandular trichomes intermixed with the pilose-strigose pubescence as exemplified by S. humilis, S. acoma, S. pinetorum and S. sarmentosa. In general, vestiture has not been too useful in delimiting taxa, although S. liebmannii var. michoacana is characterized by a pronounced subcanescent to densely strigose pubescence on the lower leaf surface, in addition to having hirsute trichomes on the upper peduncle. Sabazia leavenworthii is distinct in having villous-pilose stem

pubescence besides having a sericeous-pilose vestiture on both leaf surfaces. In a few instances achenial pubescence has proven useful in distinguishing taxa. Often, however, the achenes of a given taxon may range from being glabrous, puberulent, minutely strigose to hispidulous.

INVOLUCRE AND RECEPTACLE. The most common number of series in the involucre is two to three, but Sabazia acoma and S. microspermoides are distinguished in possessing an involucre which varies from one to two series. Sabazia multiradiata, S. liebmannii var. hintonii and var. michoacana are characterized by a three or four-seriate involucre. The phyllaries generally are broadly ovate to lanceolate-ovate with acute to acuminate apices. In very young heads the receptacle is flat but becomes increasingly convex to conical at maturity.

PALES. With the exception of a few taxa, the structure and shape of the pales are fairly uniform and consequently are not taxonomically significant. Toward the periphery of the receptacle they are usually elliptic-lanceolate, becoming narrowly lanceolate toward the center. Sabazia microspermoides is distinct in possessing spatulate pales at the periphery of the head, which change to elliptic-lenceolate structures near the center. On the other hand, Sabazia sarmentosa var. lancifolia has all linear pales.

Generally the pales have two or three linear-acuminate lobes at the apex. Sabazia liebmannii var. michoacana, however, has unlobed pales. The margins may be entire or shallowly laciniate as in S. multiradiata to lacerate-ciliate or spinulose as in S. acoma.

FLOWERS. The pistillate ray florets are fertile and occur in one series. The abaxial side of the ray ligules usually contains cyanic pigments which vary from a light to dark lavender. However, the white rays of Sabazia mullerae, S. liebmannii var. ovatifolia, and var. hintonii lack this pigment except along the margins or veins. The ligules may be quadrate to oblong or obovate with two, but more commonly three, prominent obtuse or acute teeth at the apex. All of the above mentioned shapes may exist within one population in most species; consequently ray ligule shape is of little taxonomic value. The ray tube is usually densely pilose. The style branches are ascending or recurved at anthesis; their apices are either terete or flattened, and acute or subulate.

The yellow disc florets of Sabazia are fertile, perfect and five-lobed. With the exception of Sabazia humilis and S. microspermoides whose disc florets are campanulate, the remaining taxa of Sabazia are broadly to narrowly funnelform or tubular in shape, and are fairly uniform in length. Anther and style morphology is too consistent to be of any use in distinguishing species.

ACHENES AND PAPPUS. As in most of the floral structures, achenial characters have not proven very satisfactory in delimiting taxa. Generally both the ray and disc achenes of Sabazia are obconical or obovate in outline, in addition to being striated, terete or three- to obscurely five-ridged when mature. Often the ray achenes and disc achenes near the periphery of the head tend to be laterally compressed. In Sabazia trianae and S. acoma, achenial forms may vary from obovate to narrowly ablong. On the other hand, Sabazia leavenworthii, S. liebmannii var. ovatifolia and var. hintonii are consistent in being slenderly oblong in shape. Depending upon the taxon in question, the presence and type of achenial pubescence may be significant or insignificant taxonomically. Sabazia humilis, S. multiradiata, S. mullerae, S. trianae, S. sarmentosa var. sarmentosa, and S. liebmannii var. liebmannii vary in having glabrous, puberulent to entirely strigose or hispidulous achenes. The remaining taxa are constant in pubescence characters. Consequently, achenial vestiture in this latter group can be used as a valid taxonomic criterion.

As with achenial pubescence, the presence or absence of a pappus may be variable or constant within a given taxon. Sabazia humilis, S. multiradiata, S. pinetorum, and S. sarmentosa var. triangularis may either possess or lack a pappus. The achenes of the other species, however, are consistent in being pappose or epappose. The pappus when present, is

persistent, and may be composed of scarious, obovate scales with spinulose-fimbriate apices as in Sabazia humilis, S. sarmentosa var. sarmentosa and var. triangularis. This form is identical to that of Galinsoga parviflora. On the other hand, Sabazia multiradiata, S. mullerae, S. trianae, and S. sarmentosa var. lancifolia have spinulose-ciliate, linear-lanceolate awns similar to those of Calea.

GENERIC RELATIONSHIPS AND TAXONOMIC POSITION

A clear concept of Sabazia was not perceived by early investigators, due at least in part to the few species of this genus known prior to the twentieth century. De Candolle (1836), Bentham and Hooker (1883), and Hoffmann (1894) delimited Sabazia chiefly on the basis of its lacking a pappus and its achenial morphology, placing less emphasis on other morphological features. Likewise, its subtribal assignment in the Berbesininae was determined chiefly on the basis of the above characters, despite the fact that Cassini (1829) had initially considered Sabazia and Selloa to be members of the subtribe Galinsogineae. Since 1905 when the first pappose species, Sabazia anomala Greenm., was published, three additional species exhibiting a pappus have been described. Moreover, three taxa formerly belonging to the pappose genus Calea are now regarded as species of Sabazia.

It is apparent that the presence or absence of a pappus is not useful in the circumscription of the genus Sabazia. Indeed, cytological, anatomical and morphological evidence clearly indicate that Sabazia, along with Selloa, should be transferred from the subtribe Verbesininae to the Galinsoginae. Turner and Johnston (1961) have also noted the close affinity of Sabazia with members of the Galinsogineae. Their conclusion was based on the fact that the basic number

$\underline{x}$ = 4 for Sabazia was inconsistent with other numbers in the Verbesininae, where most genera are characterized by high basic chromosome numbers varying from $\underline{x}$ = 11 to $\underline{x}$ = 30. It should be noted in this connection that the basic numbers of Sabazia and Selloa are generally in agreement with the taxa of the Galinsogineae. Chromosomal agreement concerning the relationships of these genera is further discussed in the cytological section. Additional grounds for the removal of Sabazia and Selloa from the Verbesininae are predicated on anatomical observations disclosing the lack of appressed veins in the ray corollas. This feature occurs in most members of the Galinsogineae. In view of these studies pertaining to Sabazia, I conclude that Sabazia must be referred to the subtribe Galinsogineae. Since Selloa and Tricarpha are close relatives of Sabazia, it follows that they also be placed in the Galinsogineae.

In a recent discussion of the Galinsogineae by Powell (1965), the following genera have been included: Galinsoga, Calea, Tridax and Bebbia. Another genus not mentioned by Powell is Stenocarpha, a monotypic taxon established by Blake (1917) on the basis of Galinsoga filiformis Hemsl. Stenocarpha is closely allied to Galinsoga, but is distinguished from the latter by several features which are enumerated by Turner (1965). Additional taxonomic studies on the genera of the Galinsogineae are still needed to re-assess the characters delimiting the subtribe and to properly

ascertain its position within the Heliantheae, but it seems clear that it should be expanded to include Sabazia, Selloa and Tricarpha. Furthermore, various morphological features of Jaegeria and Cuchumatanea indicate affinities with Sabazia, and future investigations may also disclose that they belong in the Galinsogineae rather than the Verbesininae.

The genus which is most closely allied to Sabazia is Selloa. A close relationship between the two genera is indicated by the nature of the heads which are hemispherical, by the 2 - 3 series of ovate phyllaries, by the deeply trilobed ray ligules which are cuneate-oblong, and by the anthers with rotund-ovate appendages and rounded to subsagittate bases. Moreover, Sabazia is characterized by chromosome numbers of $n = 4$, $n = 8$, $n = 16$, and $n = 24$ while Selloa has $n = 8$ in both species. Tricarpha also possesses several floral characters common to Sabazia, but is chiefly distinguished from the latter by much longer, oblong rays which have three very shallow apical or denticulate lobes, by prominently scarious-margined phyllaries, and by trifid pales with two very deep sinuses.

It seems likely that Selloa is more primitive evolutionarily than Sabazia or Tricarpha in view of some of the primitive characters which are common to S. plantaginea, the most primitive member of the genus. This species possess few but relatively large heads per plant, large and broad phyllaries, large and prominent ray ligules, vestigial sterile

stamens in the ray florets, numerous disc florets and large achenes. On the other hand, the genus Tricarpha appears to be more advanced than Sabazia. Tricarpha durangensis, with its perennial habit, larger leaves, and little branched inflorescence seems to qualify as the most primitive species in that genus.

Sabazia appears related to Galinsoga through S. humilis which is similar to the latter genus in possessing relatively small heads, a pappus of oblong-obovate apically fimbriate scales, trifid and slightly oblong to quadrate ray ligules, identical pales, and obpyramidal or obovate achenes which are striated. Galinsoga differs from Sabazia, however, in completely lacking the perennial habit, possessing extremely small heads (3-5 (7) mm in diameter versus 6-23 mm in Sabazia), and in having only 5 ray florets in contrast to 8-17 rays commonly found in Sabazia. Galinsoga is also distinguished from other members of the Galinsogineae in having each ray-subtending phyllary fused to two outer pales opposed to it so as to include the ray achene at maturity. This aggregration falls off the receptacle as one unit.

On the other hand, some members of Sabazia approach a few species of Calea (C. palmeri Wats. and C. elegans DC.) in possessing one or more of the following characters: a loose cymose inflorescence, an ovoid to campanulate involucre which is 3-4-seriate, obovate or narrowly subconical achenes which may be obscurely 3-5 angled, and linear-lanceolate

awns which are attenuate, lacerate and unequal. Unlike Sabazia, Calea is characterized by including mostly shrubs or stout perennial herbs, with some discoid as well as radiate species, having very unequal and often scarious phyllaries, and possessing yellow in addition to white or roseate ray ligules which are entire or denticulate at the apex. Furthermore, the basic chromosome numbers of Calea are $x = 16$ and $x = 18$, in contrast to $x = 4$ for Sabazia.

The genus Tridax appears to be more distantly related to Sabazia. The basic chromosome numbers for the former are $x = 9$ and 10 (Powell, 1965) in contrast to the basic number of $x = 4$ for Sabazia. Despite some superficial resemblances in vegetative and floral characters, Tridax can be easily distinguished from Sabazia by its bilabiate ray corollas (with inner lobelets) which are often yellow in addition to being white or roseate, the broadly tubular throat of the disc corollas, and a pappus of plumose or fimbriate scales. In only one instance has Sabazia been confused with Tridax. Sabazia trianae was originally placed in Tridax by Hieronymus.

Of all the genera within the Galinsogineae, Bebbia appears to be most distant from Sabazia. On the basis of floral characters and basic chromosome number of $x = 9$ (Powell and Turner, 1963), it appears to be allied to Calea.

EVOLUTIONARY TRENDS WITHIN SABAZIA

The general evolutionary trends within Sabazia appear to involve chiefly reduction in size and number of floral and vegetative parts and increase in number of chromosomes through polyploidy. Indirect evidence such as the frequency of endemism, paucity of individuals within populations, strong genetic isolation between species, and related species occupying distant and disjunct ranges, suggest that Sabazia is a relatively old genus. Although the present geographical ranges of the species of Sabazia might be interpreted as having resulted from migration during periods of moist and/or cool climate during the Pleistocene, it is more probable that the most important factors in the distribution of the species have been short- or long-range dispersal of propagules by means of wind or birds from one mountain range to another. These species do not constitute widespread and abundant populations. Instead they are limited to isolated, montane small populations. This situation is especially true for the more primitive species, S. multiradiata, S. mullerae and S. trianae. Furthermore, the present-day distribution of S. sarmentosa var. triangularis in Panama and Costa Rica, and S. trianae and S. acoma in Colombia can be better explained on the basis of short- or long-distance dispersal. It seems highly improbable that these plants could have

migrated through intervening low-altitude tropical zones of xeric or rain-forest conditions in Central America, since there is not a single species of Sabazia adapted to a tropical habitat.

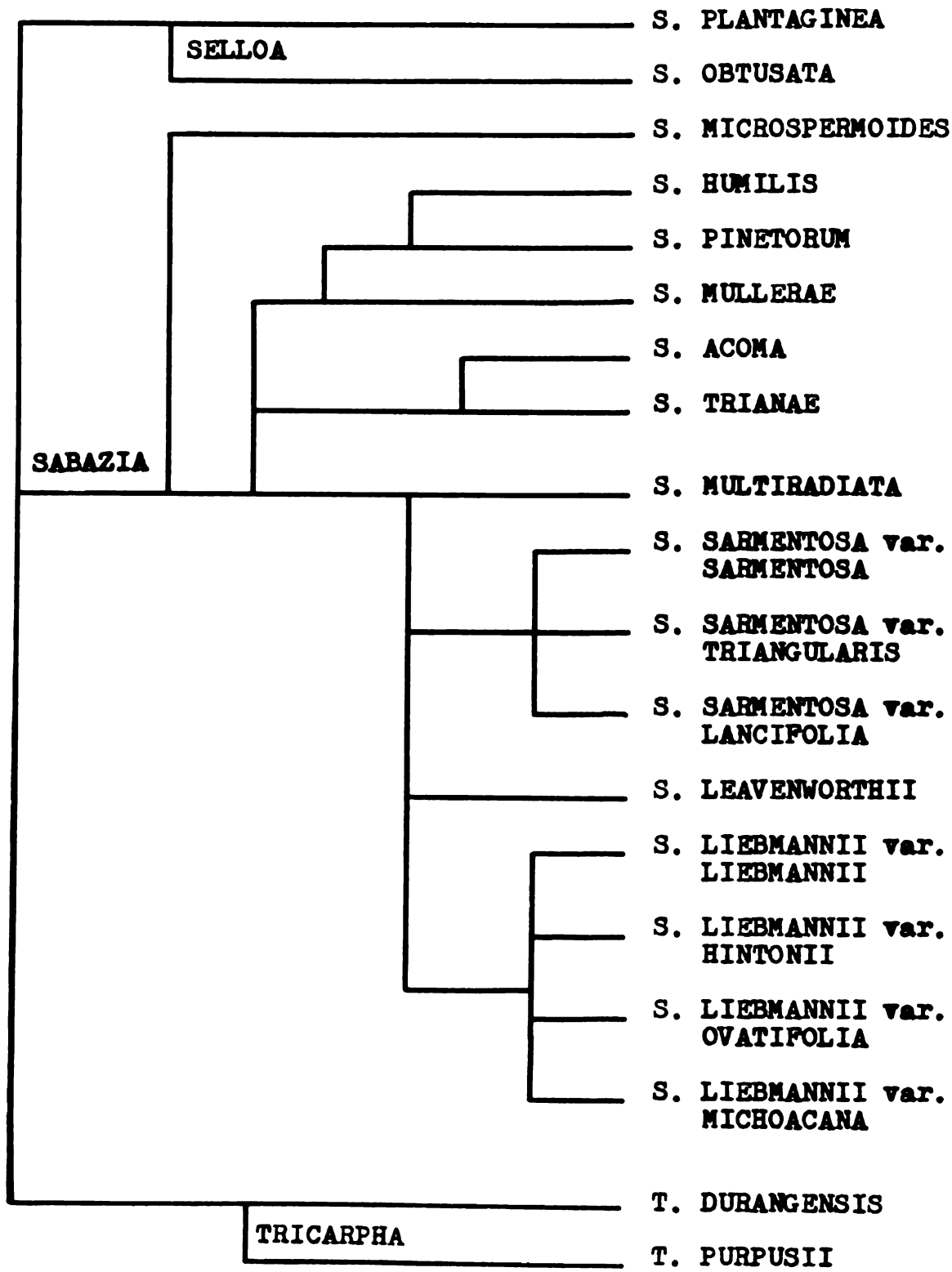
Since the majority of Sabazia species are concentrated in Mexico, it appears that this country could have been the center of origin, particularly in view of the fact that the Mexican transvolcanic belt is the center of diversity where all but three Sabazia species occur. Sabazia multiradiata, which I regard as the most primitive member of the genus, is included in this area of concentration. Furthermore, Selloa plantaginea, the most primitive species of the closely related genus Selloa, also is restricted to this area.

The primitive and advanced characters in Sabazia are enumerated in tabular form below.

primitive characters	advanced characters
1. perennial habit	annual habit
2. woody fibrous-rooted caudices	slender taproot
3. solitary to few, large heads	numerous, small heads
4. large and broad phyllaries	smaller and narrower phyllaries
5. phyllaries in 3-4 series	phyllaries in 2 series
6. large floral parts	smaller floral parts
7. numerous pappus elements	few to no pappus elements
8. glabrous achenes	pubescent achenes
9. diploidy	polyploidy

The presumed phylogenetic relationships of the taxa of Sabazia are outlined in Fig. 3. The length of the lines

Figure 3. Phylogenetic relationships of the taxa of *Sabazia*, *Selloa* and *Tricarpha*.


S. PLANTAGINEA
SELLOA
S. OBTUSATA
S. MICROSPERMOIDES
S. HUMILIS
S. PINETORUM
S. MULLERAE
S. ACOMA
S. TRIANAE
SABAZIA
S. MULTIRADIATA
S. SARMENTOSA var. SARMENTOSA
S. SARMENTOSA var. TRIANGULARIS
S. SARMENTOSA var. LANCIFOLIA
S. LEAVENWORTHII
S. LIEBMANNII var. LIEBMANNII
S. LIEBMANNII var. HINTONII
S. LIEBMANNII var. OVATIFOLIA
S. LIEBMANNII var. MICHOACANA
T. DURANGENSIS
TRICARPHA
T. PURPUSII

and clusters of branches indicate the presumed degree of evolutionary divergence or convergence. From the primitive species, S. multiradiata, evolutionary lines seem to radiate in one direction to S. mullerae in northwestern Mexico, and in another direction to S. trianae in northwestern Colombia. These three species are all comparable in having relatively large heads which are solitary or few in number, numerous and large floral parts, pubescent achenes, and a similar pappus.

The disjunction between S. mullerae and S. multiradiata may be relatively recent; that between S. mullerae and S. trianae seems to be somewhat more ancient, because from the latter species a subsequent evolutionary divergence has resulted in producing another Colombian species, Sabazia acoma. Despite the fact that S. acoma is sympatric with S. trianae, the availability of numerous, isolated montane habitats with differing micro-environments could have facilitated speciation of these populations.

Sabazia trianae is separated from S. multiradiata by a distance of about 1900 miles. Both the former and S. mullerae probably had ample opportunity during the late Tertiary or Pleistocene to travel by jumps from one mountain to another. Another precursor of the S. mullerae line probably developed into the Guatemalan species S. pinetorum. At a later time from the same stock S. humilis evolved in the Mexican transvolcanic belt. It is interesting to note

in this connection that S. multiradiata, S. mullerae, and S. pinetorum have a chromosome complement of n = 8, which helps to suggest their origin from a common ancestral stock.

Although Sabazia humilis appears to be related to S. pinetorum on the basis of similar leaf and floral morphology, it seems to be a more actively evolving taxon undergoing further evolutionary reduction; this trend is exemplified by the annual habit, the slender taproot which became reduced from the lignescent caudex, and the change from larger and more numerous floral parts to fewer and smaller floral parts.

Another evolutionary trend from the S. multiradiata complex appears to have occurred in S. leavenworthii, an endemic to Cerro Tancitaro in Michoacan. Speciation in this group was most likely accomplished through polyploidy (S. leavenworthii with n = 16 versus n = 8 in S. multiradiata) in addition to geographical isolation. Sabazia leavenworthii probably is adapted to disturbed sites as evidenced by its presence in volcanic ash.

Ancestral populations of Sabazia liebmannii and S. sarmentosa, both with a chromosome complement of n = 24, also must have undergone evolutionary specialization from a more generalized S. multiradiata line. As in S. leavenworthii, the availability of numerous and diverse montane habitats, and the effects of polyploidy probably provided the necessary prerequisites for speciation and for the estab-

lishment of new varieties. An additional evolutionary factor not to be overlooked is the possibility of hybridization. Populations of the S. multiradiata type (n = 8), through hybridization and polyploidy with populations representative of the S. leavenworthii stock (n = 16), could have created a new population prototype with a chromosome number of n = 24. Although the ranges of S. sarmentosa and S. liebmannii partially overlap in Mexico, the four varieties of the latter are restricted to the southwestern and southern parts of Mexico in disturbed habitats of sandy loam reddish clay soil. Sabazia sarmentosa, however, extends into Guatemala, Costa Rica, and Panama. In the highlands of the latter two countries, S. sarmentosa var. triangularis appears to have evolved from the southernmost populations of var. sarmentosa. This change most likely occurred during the Pleistocene after the population became isolated from var. sarmentosa. At present, these two varieties are separated by a distance of at least 500 miles.

Sabazia microspermoides seems to be the only species whose evolutionary trends parallel those of S. humilis through convergent evolution. Both species have the annual habit, and very small and reduced floral parts. Sabazia microspermoides does not appear to be very closely related to any extant taxon of Sabazia.

Discussion of the generic relationship of Selloa and Sabazia is included in the section on Generic Relationships

and Taxonomic Position. It should be noted here, however, that Selloa plantaginea seems to be even more primitive than Sabazia multiradiata. Its more primitive characters include much larger heads, larger floral parts and vestigial sterile stamens in the ray florets. On the other hand, the genus Tricarpha appears to be more advanced than Sabazia. Tricarpha durangensis, with its perennial habit, larger leaves, and little branched inflorescence seems to qualify as the most primitive species in that genus.

KEY TO THE GENERA

A. Pales linear-setiform, 0.1-0.2 mm wide; leaves in basal rosettes and cauline; outer phyllaries herbaceous. . . . . Selloa

AA. Pales not linear-setiform, more than 0.2 mm wide; leaves cauline only; outer phyllaries herbaceous or scarious along the margins . . . . . B

B. Inside pales trifid with 2 deep sinuses to the base or 3/4 the pale length, lateral acuminate lobes equal or 3/4 the length of the middle lobe; outer phyllary margins conspicuously and broadly scarious; ray apices denticulate or shallowly bilobed or trilobed, ligules roseate-purple on both surfaces or white above and below; disc achenes epappose . . . . . Tricarpha

BB. Inside pales entire or with 1 or 2 unequal acuminate lobes 1/8 to 1/2 the pale length; outer phyllary margins herbaceous (rarely scarious, if so very inconspicuous); ray apices prominently trifid (rarely bifid), ligules always white above, roseate-purple or white below; disc achenes pappose or epappose. . . Sabazia

TAXONOMY OF SABAZIA

Sabazia Cass. Dict. Sci. Nat. 46: 480. 1827. Eclipta sensu H.B.K. Nov. Gen et Sp. 4: 264 Fig. 394. 1820. Baziasa Steudel, Nom. Bot. ed. 2. 1: 192. 1840.

Annual or perennial, caulescent herbs with tap roots, fibrous roots or fibrous-rooted caudices; stems erect, ascending, decumbent or procumbent, sometimes pendent, rarely rooting at the nodes, striate and grooved, glabrous to densely pilose-strigose or hirsute, rarely with glandular-tipped trichomes, especially on the peduncles and outer bracts; leaves simple, opposite, sessile to petiolate, ovate to lanceolate, elliptical and linear, margins entire, serrate to remotely denticulate, sometimes ciliate; heads solitary or inflorescence a few-headed paniculate cyme; heads radiate, cernuous, often subtended by upper cauline leaves, long to short-pedunculate; involucre campanulate or hemispherical; phyllaries imbricate, in 2 or 3 series, rarely 1 or 4 series, outer series often carinate, broadly ovate to linear-lanceolate, apices acute or lacerate-ciliate, subequal in length, often roseate to purple-tinged toward the apices, inner phyllaries membranaceous, lacerate-ciliate mostly above the middle; receptacle convex to conical at maturity, paleaceous; pales persistent, scarious, elliptic-lanceolate to lanceolate,

acute to acuminate, entire or with 1 or 2 shallow lateral lobes; ray florets pistillate and fertile, in one series, tubular at the base with sparse to dense trichomes, ligules white above, commonly roseate-purple below, distinctly trifid (rarely bifid) at the apices; disc florets perfect, fertile, the corolla yellow, narrowed below into a relatively broad tube, slightly to densely pubescent, abruptly forming a tubular to campanulate throat, lobes equal, ovate-acute or obtuse, erect to reflexed; style branches oblique or recurved, slender and subterete or flattened on the inner surface, apices acute, rarely acuminate or with obscure subulate tips; anthers rounded to subsagittate at the base, appendages cordate-ovate; achenes obovate or turbinate, terete to obscurely 3-5 ridged, often laterally compressed toward the periphery of the head, black at maturity, glabrous to moderately pubescent with ascending trichomes; pappus absent or present, subequal or equal, of obovate apically spinulose-fimbriate scales, or of subplumose linear-lanceolate awns; basic chromosome number $x = 4$; type species, Sabazia humilis (H.B.K.) Cass.

Key to the Species of *Sabazia*

A. Plants annual; pappus, when present, of 5-10 obovate spinulose fimbriate scales; decumbent to ascending, never prostrate or trailing . . . . . B

B. Ray florets 4 to 6 (usually 5), ligules obdeltoid to oblong, ligule lobes deeply cleft, over 1/3 to 1/2 the ligule length; plants to 9.5 cm high. . . . . 10. *S. microspermoides*

BB. Ray florets 7 to 13, ligules quadrate to oblong, ligule lobes less than 1/3 the ligule length; plants 12-45 cm high (rarely below 12 cm). .9. *S. humilis*

AA. Plants perennial; pappus, when present, of 15-30 linear-lanceolate awns with spinulose-ciliate margins; decumbent, ascending, erect, prostrate or trailing . . . C

C. Leaves entire or with 2-4 pairs of minute teeth, 0.5 mm high or less, sessile; plants of Colombia. . . D

D. Disc pappus of 10-20 unequal awns; disc achenes pubescent; leaves elliptic-lanceolate or lanceolate, lamina 2.2-17 mm wide; leaf and outer phyllary margins without glandular-capitate trichomes . . . . . .3. *S. trianae*

DD. Disc pappus absent; disc achenes glabrous; leaves linear-lanceolate, lamina 1.2-5.5 mm wide; leaf and outer phyllary margins with glandular-capitate trichomes. . . . . .4. *S. acoma*

CC. Leaves serrate or broadly toothed, sessile or petiolate; plants of Mexico and Central America. . . . . E

E. Plants with thickened, lignescent, erect or oblique rhizomes with lateral roots; heads commonly 3 or more in a loose subcyme; disc florets epappose . . . . . 8. S. liebmannii

EE. Plants with thin rhizomes or fibrous roots; heads solitary (except for S. multiradiata in which some specimens are subcymose); disc florets pappose or epappose. . . . . F

F. Plants prostrate, pendent, trailing or decumbent (rarely erect), generally in moist habitats, often with adventitious roots; leaves acuminate, petiolate; disc achenes glabrous or sparsely hispidulous along the margin. . . . . 7. S. sarmentosa

FF. Plants erect, ascending or decumbent, in mesic or semi-arid habitats; leaves usually acute, sessile or petiolate, disc achenes hispidulous over the entire surface or sparsely so along the margins . G

G. Leaves petiolate; stems densely villous-pilose near the heads; disc achenes always epappose, appressed-hispidulous over the entire surface . . . . . 6. S. leavenworthii

GG. Leaves sessile (sometimes subsessile); stems densely appressed-pilose near the heads; disc achenes glabrous when epappose but entirely or marginally

hispidulous when pappose. . . . . H

H. Leaves broadly ovate below to lanceolate-ovate above, bases obtuse or truncate, lamina 2-5.5 cm long, 0.5-3.5 cm wide . . . . 1. *S. multiradiata*

HH. Leaves elliptic-lanceolate or elliptic-ovate, bases cuneate, lamina 0.9-3.8 cm long, 0.2-1.7 cm wide. I

I. Aerial stems arising from slender running rootstocks; leaves petiolate; involucre 2-seriate; ray florets 8 or fewer; plants of Guatemala . . . . . 5. *S. pinetorum*

II. Aerial stems arising from small, short bulbous rootstocks or fibrous-rooted caudices; leaves sessile; involucre 3- (-4) seriate; ray florets 8 or more (usually 10 to 16); plants of northeastern Mexico. . . . . 2. *S. mullerae*

1. Sabazia multiradiata
(Seaton) Longpre, comb. nov.

Calea multiradiata Seaton, Proc. Amer. Acad. 28: 120. 1893. Type. MEXICO. PUEBLA: Pine woods, 10,000 ft, 6 Aug 1891, Seaton 167 (GH, holotype!; F, US, isotypes).

Sabazia liebmannii var. heterocarpa Robins. & Greenm. (Type is Seaton 167 in part).

Plants perennial, branching from a short, fibrous-rooted caudex, 23-66 cm high, erect or ascending; stems striate, with appressed, white, soft trichomes 0.5-0.75 mm long, becoming more densely pubescent toward the apex, often reddish-purple; leaves opposite, usually sessile but sometimes subsessile, petioles 1-3 mm long, laminae broadly ovate to lanceolate-ovate above, 2-5.5 cm long, 0.5-3.5 cm wide, apices acute, bases obtuse or truncate, margins crenate-dentate with 2-4 (-5) pairs of remote callous-tipped teeth, minutely strigose-pilose to scabrescent on both surfaces but more densely so below; peduncles 5.5-14 (-31) cm long, pubescent as on the stem but more densely so; heads 1-3, hemispherical, often subtended by a bract along the peduncle, 2-2.5 cm wide (including the rays), born singly on peduncles or in a loose subcyme; receptacle paleaceous, conical, 2-3 mm wide, 2-3 mm high, pales persistent, scarious, glabrous, elliptic-lanceolate, acuminate, 1.5-4 mm long, 0.4-1 mm

wide, trilobed, bilobed or entire, shallowly laciniate along margins; involucre 3-4 seriate, bracts imbricate, equal or subequal, the outer broadly ovate to lanceolate-ovate, 3-5 (-6.5) mm long, (1-) 2-3.2 mm wide, apices acute, upper margins entire to minutely ciliate and often reddish-purple, glabrous, 6-10-nerved, carinate toward the base, inner bracts narrowly ovate, 4-5.5 (-7.3) mm long, 1.5-2.4 mm wide, membranaceous, usually more ciliate near the apex than the outer; rays 7-17, pistillate, fertile, tubular at the base for 1-2 mm. densely pilose, ligules white above and roseate-purple below, obovate to oblong-obovate, 3.5 -8 (-11) mm long, 1.8-5 mm wide, with 3 (rarely 2) acute or obtuse apical lobes, (0.5-) 1-4 (-8) mm long; ray style branches terete, tapering to a point; disc corollas yellow, perfect, funnelform to tubular, tube 0.5-1 mm high, pilose, the limb 1.5-2 mm long, 0.6-1 mm wide, the lobes acute, minutely papillate inside and pubescent on the outside; anthers 1-1.2 mm long, appendages rotund-ovate, subsagittate at the base; style branches recurved, subulate, pubescent at the apex; ray achenes obconical to compressed, 1-2 mm long, epappose, glabrous or puberulent to minutely strigose along the ridges, disc achenes similar but more commonly strigose or hispidulous over the entire surface, pappus, when present, of 12-20 unequal subplumose linear-lanceolate awns or scales, 1-2.5 mm high; chromosome number $\underline{n}$ = 8.

ECOLOGY AND DISTRIBUTION. In open, montane pine and oak forests in sandy loam soil, at elevations of 2100 to 3500 meters. Flowering from July to September. Distributed from central Puebla southward to central Oaxaca (Fig. 5).

SPECIMENS EXAMINED. MEXICO. OAXACA: In partial shade, loamy soil, mtns along route 175, ca 21 miles N of junction with route 190, 26 July 1960, King 3499 (TEX, UC); Sierra de San Felipe, 10,000 ft, 19 Sept 1894, Pringle 4921 (GH, MO, MSC, UC, US). PUEBLA: In open forest of Pinus, Arcos, Ojo de Agua, Sierra Negra, 5 July 1938, Balls 4458 (US); Cerro Verde, in the vicinity of San Luis Tultitlanapa, Puebla, near Oaxaca, July 1908, Purpus 3110 in part (F, 2 sheets, GH, NY, UC, US); Cerro del Oro, Aug 1909, Purpus 3837 (F, GH, UC, US); oak forest, 7000-8000 ft alt, Cerro del Oro, Aug 1909, Purpus 3838 (UC); San Simon, elev 8000-9000 ft, Aug 1909, Purpus 3960 (F, two sheets, MO, UC, US); near Chalchicomula, 24 July 1901, Rose & Hay 5650 (GH, 2 sheets, US); pine woods, Mt Orizaba, 6 Aug 1891, Seaton 167 (GH, holotype; F, US, 2 sheets); roadside bank above Sierra Negra, above Serdan, Cabecero, 25 Sept 1944, Sharp 44998 (NY).

Sabazia multiradiata exhibits the same variation as S. humilis and S. pinetorum in having both pappose and epappose forms within the same population. It resembles S. mullerae in having large heads, numerous ray florets, sessile leaves, a 3-4-seriate involucre, pappose disc achenes with

unequal subplumose, linear-lanceolate awns, and a chromosome number of n = 8. In fact, a larger broad leafed form of S. mullerae (Beaman 4492) is very similar to S. multiradiata. However, S. mullerae differs in possessing typically elliptic-ovate leaves near the base of the stem, solitary heads only, and pappus awns which are approximately twice the length of those in S. multiradiata.

Sabazia liebmannii appears to be distantly related to S. multiradiata and is distinguished from the latter in generally having petiolate, elliptical to lanceolate-ovate leaves with cuneate bases, stout, woody rootstocks, epappose and glabrous achenes, ray flowers never exceeding eight, and a chromosome number of n = 24. In contrast, S. multiradiata is typically characterized by sessile or subsessile, ovate or lanceolate-ovate leaves with obtuse bases, remote dentate margins, fibrous roots or a thin, fibrous-rooted caudex, and usually pappose, pubescent disc achenes. The species are sympatric in the Cerro San Felipe and Cerro Verde regions of Oaxaca.

Confusion has existed in distinguishing the above two species, as in the case of Purpus 3110 (F, no. 247339) where both species were mounted together. Another example is the unique population of S. liebmannii var liebmannii based on the collection of Smith 288 from Cerro San Felipe. These plants appear to be intermediate morphologically between S. liebmannii var. liebmannii and S. multiradiata. It is

possible that the Smith collection could represent a hybrid population arising from these two species since they are both found within the same geographical area. Moreover, the extremely large heads may be the result of heterosis. Additional collections as well as cytological and genetical studies are needed to resolve this problem.

2. Sabazia mullerae Blake

Sabazia mullerae Blake, Jour. Wash. Acad. Sci. 32: 149. 1942. Type. MEXICO. NUEVO LEON: Open chaparral on upper west slope of Sierra de la Cebolla, 21 Aug 1939, C. H. Muller 2902 (US, holotype!; GH, UC, isotypes).

Perennial, with slender fibrous roots, from a fibrous-rooted caudex 2-4 mm thick; stems decumbent to ascending, simple or branching, 11.5-36.0 cm long, 1-2 mm wide, sparsely appressed-pilose below to more densely so near the apex; leaves opposite, elliptic-ovate below to lanceolate-ovate above, apices acute, bases cuneate, margin with 2-3 pairs of callous-tipped teeth, 0.5-1.3 mm long, sparsely pilose or pilose-strigose on both sides or hirsute, lamina 0.9-3.8 cm long, (1.5-) 3-17 mm wide, sessile or subsessile, petiole 1-2 mm long, densely pubescent, narrowly margined; peduncle 1-12 cm long, moderately to densely pilose; heads terminal, 1-12 per plant, hemispherical; receptacle conical,

4 mm long, 3.5 mm wide at the base, pales elliptic-lanceolate near the periphery to linear-lanceolate toward the center, 3-5.5 mm long, 1 mm wide; involucre 3- (-4) seriate, 7-12 mm wide, 3-6 mm high, subequal, outer phyllaries broadly ovate to lanceolate-ovate, apices acute, sometimes lower one-half green and upper one-half roseate, (3-) 4-8 mm long, (1.5-) 2-4.8 mm wide inner phyllaries lanceolate-ovate to ovate, 5-7.2 mm long, 2-3.8 mm wide, 5-nervate, margins glabrous, entire to minutely ciliate, green to subhyaline, upper half often roseate; ray florets (8-) 11-16, white above and below (sometimes roseate along veins below), tube 1.8-3 mm long, moderately appressed pilose, ligules cuneate-obovate to quadrate, 3.8-6.8 mm long, 3.8-5 mm wide, with 3 acute or obtuse lobes, 1.5-2.2 mm long, style branches recurved, acute, styles 2.5-3 mm long, disc florets ca 35-140, narrowly funnelform, tube 1-1.2 mm, moderately to densely pilose (sometimes hirtellous), limb 2-2.2 mm long, 5-lobed, acute, papillate inside; anthers 1.2-1.5 mm long, rounded to sub-sagittate bases, appendages rotund-ovate; styles terete, 2.8-3.3 mm long, surrounded at the base by a nectary, style branches flattened, acute, minutely papillate on the outside; ray achenes terete, obovate, obscurely 3-ridged, 1.5-2 mm long, glabrous, epappose; disc achenes obovate (1.5-) 2 mm long, sparsely hirtellous along the margins to entirely hirtellous, pappus of about 24 unequal, lanceolate-linear acuminate awns with ciliate margins, 2-3.4 mm high; chromosome

number n = 8.

ECOLOGY AND DISTRIBUTION. In valleys interspersed with arroyos and alluvial fans, open chaparral or rocky meadows associated with pine forests at elevations of about 3200 meters. Collected in flower in August and September. Known only from northeastern Mexico in the states of Nuevo Leon and Tamaulipas (Fig. 5).

SPECIMENS EXAMINED. MEXICO. NEUVO LEON: Cerro Potosi, east side of mtn above Diez y Ocho de Marzo, along NE trail to summit, 13 Sept 1960, Beaman 4473 (MSC); Cerro Potosi, east side of mtn near Km 18, on road to Telefonas de Mexico installation, 16 Sept 1961, Beaman 4492 (MSC); Cerro Potosi, east side of mtn at Km 18, on road to Telefonas de Mexico installation, 20 Sept 1961, Beaman 4514 (MSC); Cerro Potosi, east side of mtn at km 18, 3 Aug 1962, Longpre 503 (MSC); upper west slope of Sierra de la Cebolla, 21 Aug 1939, Muller 2902 (US, holotype; GH, UC, isotypes); Tamaulipas: near town of Miquihuana, 8 Aug 1941, Stanford, Retherford & Northcraft 773 (DS, GH).

Sabazia mullerae appears to be closely related to S. pinetorum and S. multiradiata. The former is similar in habit, possessing elliptic-ovate to lanceolate-ovate leaves with identical margins, pappose disc achenes with unequal lanceolate-linear awns, and the same chromosome number.

However, S. pinetorum differs in being more decumbent, non-ascending, distinctly petiolate, having a two-seriate involucre, ray florets not more than eight, and having shorter pappus awns. The relationship of S. mullerae to S. multiradiata has been discussed under the latter species.

Although S. trianae, an endemic of Colombia, has the southernmost distribution of all Sabazia species, it may be distantly related to S. mullerae. It also possesses unequal, linear-lanceolate awns about the length of the disc corollas. In addition, its leaves are similar in being approximately the same size and elliptic-lanceolate in shape. It is distinguished from S. mullerae in sporadically having a ray pappus, and having more pubescent leaves, fewer (eight) ray florets, and a two-seriate involucre.

3. Sabazia trianae (Hieron.) Longpre, comb. nov.

Tridax trianae Hieron. Bot. Jahrb. 21: 350. 1895. Calea longipes Blake, Jour. Wash. Acad. Sci. 18: 34. 1928. Type. COLOMBIA. CUNDINAMARCA: Anaporina, Bogota, elev 2600 m, Triana 1422 (BM, lectotype; K, isotype; MSC photo of syntype in B [destroyed] from F neg. 15413).

Plants perennial, simple or branching from the base, to 81 cm tall, from a slender or oblique rootstock of fibrous

roots; stems (including peduncles) decumbent to ascending, very sparsely to densely pilose, the trichomes becoming more dense and appressed near the heads, dark roseate-purple, sometimes with a few black, glandular-capitate trichomes intermixed; leaves opposite, elliptic-lanceolate or lanceolate, bases cuneate to obtuse, apices acute, callous-tipped, margin entire or sometimes with 2-4 pairs of short callous-tipped teeth, ciliate, sparsely to densely strigose-pilose to hirsute-strigose above and below, 1-5 cm long, 2.2-15 (-17) mm wide, sessile; heads terminal or axillary, 1 to 4 per plant, hemispherical; phyllaries in 2 equal or subequal series, (6-) 9-12 mm in diameter, 4-6 mm high; outer phyllaries ovate, apices sometimes ciliate, acute to obtuse, 3-5 mm long, (1.5-) 2-3 (-4) mm wide, 5-nerved, glabrous, dark purple near the apex and margin, yellowish-green below with purplish venation, entire; inner phyllaries ovate or lanceolate-ovate, 4-6 mm long, 1.8-2.8 (-3.8) mm wide, glabrous, entire, hyaline; pales persistent, elliptic-lanceolate near the periphery to narrowly lanceolate toward the center, acuminate, entire, 3.2-5 (-6.3) mm long, 0.5-1.6 mm wide, scarious; receptacle convex to conical, 2.5-4 mm long, 2.5-3 mm wide; ray florets 8, corolla tubes (1.5-) 1.8-3 mm long, sparsely to densely pilose, ligules obovate to oblong or quadrate, white above, roseate-purple below, 5-11 mm long, (3.7-) 4.2-6 mm wide, the apical lobes obtuse or acute, (0.5-) 1-2.2 mm long, style 2.5-4 mm long, style branches recurved,

flattened, acute; disc florets 30-90, narrowly funnelform, corolla tubes (0.8-) 1-2.7 mm long, sparsely to densely appressed pilose, limb (1-) 2-3 mm long, with 5 acute lobes, 0.4-0.5 mm long, glabrous or minutely pubescent outside; anthers 1-2 mm long, rounded or subsagittate, appendages rotund-acute, filaments long, attached 1/4 or 1/3 the distance from the corolla base, style 2.7-3.5 mm long, style branches recurved, acute, papillate on the outside, and along the margins; ray achenes obovate or obconical, somewhat laterally compressed, obscurely 3-angled, 1.8-2.2 mm long, glabrous to hirsute, 9-nerved, black, pappus absent, or if present, of 5 to 10 unequal linear-lanceolate, attenuate, ciliate awns, (0.2-) 0.5-2 mm long; disc achenes obovate or narrowly obconical, obscurely 3-5 angled, (1.3-) 1.8-2.2 mm long, black, striate, appressed pilose or hirtellous, pappus of 10-20 linear-lanceolate awns, attenuate, ciliate, 1.8-4 mm long, unequal.

ECOLOGY AND DISTRIBUTION. In subalpine woods, savannas and pastures among shrubs in humid, rocky soil at elevations from 3000 to 3850 meters. Flowering appears to be more common from May through October, although a few specimens have been collected in flower from November through January. Restricted to the Cordillera Oriental within the Colombian departments of south-central Boyaca, northern Cundinamarca, and northeastern Santander (Fig. 4).

SPECIMENS EXAMINED. COLOMBIA. BOYACA: Hacia La Cueva, en la Zanja, elev 3700 m, 13 Sept 1938, Cuatrecasas 1638 (F, US); Cordilleras Oriental, Quebrada de Becerra, to the NE of Duitama, 4 Aug 1940, Cuatrecasas 10394 (F); Sierra Nevada del Cocuy, around Hacienda Ritacuba, elev ca 3600 m, July 1929, Grubb & Curry 129 (US). CUNDINAMARCA: Paramo de Choachi, elev 3200 m, 27 Dec 1927, Bro. Apolinar-Maria 398 (F); Tequendama, 25 July 1929, Bro. Apolinar-Maria 399 (F); Tequendama, 25 July 1929, Bro. Apolinar-Maria 400 (F); Cerro Monserrate (Bogota) 26 April 1951, Castaneda 2488 (F); Monserrate, near Bogota, slopes near the summit, elev 3170 m, 6 Oct 1938, Cuatrecasas 281 (F, US); western slopes of Paramo de Cruz Verde, elev 3150 m, 7 Oct 1938, Cuatrecasas 433 (F); Macizo de Bogota, Cerro entre Quebradad de las Delicias y la de las Niñas, 25 June 1939, Cuatrecasas 5639 (F, US); Chipaque, July 1916, Dawe 396 (US); Guadalupe, Bogota, 15 May 1947, Haught 5721 (US); Guadalupe, above Bogota, elev ca 3000 m, 1 Nov 1949, Haught 6693 (US); Bogota Plateau, Monserrate, 22 Dec 1926, Niemeyer 136 (US); Bogota Plateau, Monserrate, 22 Dec 1926, Niemeyer 137 (US); Bogota, 14 May 1948, Regis 53 (F); Cordillera Oriental, Usme Exp. Stat. ca 10 km south of Usme, 15 June 1950, S. G. Smith, Idrobo & Jaramillo 1043 (US). CUNDINAMARCA ?: Bro. Ariste-Joseph A 773 (US). SANTANDER: Paramo de Santurban, elev ca 3000 m, 27 Aug 1948, Barclay & Araque 18S172 (US); Paramo de Vetas, elev ca 3400-3700 m, 16 June 1927, Killip & Smith

17404 (US); Paramo Rico near Vetas, elev ca 3750-3850 m, 18 June 1927, Killip & Smith 17661 (US); Paramo de las Coloradas, above La Baja, 27 Jan 1927, Killip & Smith 18439 (US). DEPARTMENT ?: N. Grande, Linden 61 (US).

Georg Hieronymus (1895) originally described this species in the genus Tridax. Blake (1928), after having examined the type, transferred it to the genus Calea because of its linear-lanceolate and lacerate-ciliate pappus awns, typical of Calea. Since Hieronymus (1895) had previously described a Calea trianae, Blake named the species C. longipes. Powell (1965) concurred with Blake in excluding the species from Tridax. Hieronymus mentions two collections upon which he based Tridax trianae, Triana 1422 and a collection numbered 176b without a collector's name (although Blake (1928) presumably attributes the latter collection to Stuebel since most of the plants were collected by him). Hieronymus did not cite where his two collections were deposited. It is quite likely that the type species was left in B and was destroyed during World War II. Blake refers to the type number of S. trianae (Triana 1422) from the British Museum and Kew herbaria (probably isotypes) without designating a holotype. Therefore, I have designated Triana 1422 in the British Museum as lectotype.

Despite the Calea-like pappus, characters typical of Sabazia, such as campanulate heads, broadly obovate achenes, ray ligules with three prominent teeth, and the roseate color under the rays, warrant placing this species in Sabazia. Sabazia acoma is a closely allied species which is distinguished by linear-lanceolate leaves and epappose achenes.

4. Sabazia acoma (Blake)
Longpre, comb. nov.

Calea acoma Blake, Jour. Wash. Acad. Sci. 25: 317. 1935. Type. COLOMBIA. NORTE DE SANTANDER: In open place, western slope of Paramo del Hatico, en route from Toledo to Pamplona, elev 2800-2900 m, 13 Mar 1927, Killip & Smith 20721 (US, holotype!; F, isotype).

Plants perennial, ascending to erect, branching near the base and along the stem, exceeding the main stem, arising from a slender tap root; stems up to 40 cm long, green or reddish-purple, striate, with very sparsely pilose to moderately pilose trichomes intermixed with glandular-capitate

trichomes, the heads usually reddish-purple to dark purple; leaves opposite, linear-lanceolate, base truncate, apex acute, margins slightly revolute, entire except for 1-2 pairs of minute callous-tipped teeth, glandular-ciliate, 1.5-5 cm long, 1.2-5.5 mm wide, glabrous to sparsely pilose above and below, 3-nerved, the midrib more prominent than the laterals; heads solitary or ternate at stem and branch apices, 3-6 per plant, hemispherical; involucre (1-) 2-seriate, 8-10 mm wide, 5-6 mm high, outer phyllaries lanceolate-ovate, acute or obtuse, apices 3-6 mm long, 1-2 mm wide, herbaceous, glabrous to very sparsely pilose, margins entire and ciliate, inner phyllaries ovate to elliptic-lanceolate, 4.2-4.5 mm long, 1.8-2.2 mm wide, glabrous, herbaceous, membranaceous, margins entire or sometimes minutely spinulose; receptacle pyramidal, 2 mm long, 2 mm wide at the base, pales persistent, elliptic-ovate at the periphery to narrowly lanceolate toward the center, 3.2-4.5 mm long, 0.2-1.0 mm wide, margins lacerate-ciliate or spinulose; ray florets 5-8, white, tube 1.8-2.5 mm long, moderately pilose-hirtellous, ligules obovate-oblong or cuneate-oblong, 6.5-8 mm long, 3-4 mm wide, unequally 3-lobed, apices obtuse, 1-2 mm long, 0.5 mm wide, styles 3.2-4 mm long, style branches recurved, acute at the apex, papil-late on the inner stigmatic surface and margins; disc florets about 33, narrowly to broadly funnelform, tube 1-1.5 mm long, pilose-hirtellous, limb 1.5-1.8 mm long with 5 acute lobes, greenish-yellow, 0.3-0.5 mm long; anthers 1.2-1.4 mm long,

bases subsagittate, appendages rotund-acute; styles 2.5-5 mm long, style branches similar to those of ray florets; ray achenes epappose, obovate (or oblong-obovate) to narrowly obconical, black, striate, glabrous, 2 mm long when mature; those of disc florets similar.

ECOLOGY AND DISTRIBUTION. From the three collections available, flowering appears to occur from January through March (perhaps longer). In the northern part of the Eastern Cordillera of Colombia at elevation from 2800 to 3700 meters in northeastern Santander and southern Norte de Santander. Sympatric with S. trianae in the northern range of the latter (Fig. 4).

SPECIMENS EXAMINED. COLOMBIA. NORTE DE SANTANDER: Eastern Cordillera, 20-22 Feb 1927, Killip & Smith 19637 (US); Eastern Cordillera, western slope of Paramo del Hatico, en route from Toledo to Pamplona, elev 2800-2900 m, 13 March 1927, Killip & Smith 20721 (US, holotype, F). SANTANDER: Eastern Cordillera, Paramo de las Puentes, above La Baja, elev 3500-3700 m, 25 Jan 1927, Killip & Smith 18230 (US).

The relationships of Sabazia acoma have been discussed under the systematic treatment of S. trianae. Blake (1935), who regarded S. acoma as a Calea, thought it might be an epappose variety of S. trianae. Both species are endemic to the Eastern Cordillera and are sympatric in the department

of Santander. Future field collections and investigations are necessary in order to further clarify their taxonomic position. For the present, I recognize Sabazia acoma as a species which can be readily distinguished from S. trianae by its linear-lanceolate leaves, and epappose achenes.

5. Sabazia pinetorum Blake

Sabazia pinetorum Blake, Brittonia 2: 347. 1937. Type. GUATEMALA. HUEHUETENANGO: Open pine woods, Sierra Cuchumatanes, 10900 ft, 14 Sept 1934, Skutch 1234 in part (GH, holotype!; F, US, isotypes).

Sabazia pinetorum var. dispar Blake, Brittonia 2: 348. 1937. Type. GUATEMALA. HUEHUETENANGO: Open pine woods, Sierra Cuchumatanes, 10900 ft, 14 Sept 1934, Skutch 1234 in part (GH, holotype!).

Plants perennial, decumbent, simple or subsimple, to 63 cm high, from a slender horizontal rootstock with fibrous roots; stems sparsely pilose, striate, often reddish-purple; leaves opposite, elliptic-lanceolate (rarely elliptic-ovate) below to linear-lanceolate above, cuneate (rarely obtuse), apices acute, margin entire to shallowly crenate with 2-3 pairs of callous-mucronulate teeth, sometimes ciliate, lamina (0.8-) 1.2-3.1 cm long, 0.2-0.7 (-1.2) cm wide, sparsely pilose to densely strigose-pilose above and below but more densely so along the midrib, 3-nerved, commonly with a prom-

inent midvein below; petioles 2-4 (-6.5) mm long, hirsute; peduncles 5-15 cm long, with white pilose trichomes becoming more dense and appressed near the head, sometimes with purple glandular-capitate trichomes near the head; heads terminal, solitary, suboval to hemispherical; involucre 2- (-3) seriate, unequal, 6-10 mm wide, 4-6 mm high, outer phyllaries ovate or elliptic ovate, obtuse (rarely acute) 3.5-5 mm long, (1.5-) 2-3 mm wide, margins entire, rarely subglandular, lacerate or ciliate, glabrous, membranaceous, 5-striate, herbaceous, often roseate-purple along the margins and the upper half, inner phyllaries somewhat longer and narrower, elliptic-ovate or oblong-ovate, acute, 4-6 mm long, 1.8-3 mm wide, glabrous, herbaceous, margins scarious, entire to minutely subglandular lacerate-ciliate; receptacle conical, 2.5 mm long, 2 mm wide; pales persistent, elliptic-lanceolate near the periphery, linear-lanceolate at the center, acuminate, sometimes with 1 or 2 lateral lobes, (2.2-) 2.7-5 mm long, (0.2-) 0.7-1.5 mm wide, rarely purplish at the apex; ray florets 8, pistillate, fertile, tubes (1.5-) 2 mm long, sparsely to moderately pilose, ligules broadly obovate or oblong, white above, roseate-purple below, 5.5-10 mm long, 2.5-5 mm wide, with 3 apical acute or obtuse teeth, 0.7-2.5 mm long; styles 2-2.5 mm long, style branches recurved, flattened, acute; disc florets ca. 60, yellow, fertile, funnelform, tube 1 mm long, sparsely to densely pilose-hirtellous, limb 1.5-2 mm long, sometimes pilose near the

base, lobes 5, acute, sparingly puberulent outside, minutely papillate inside, 0.4 mm long; anthers 1-1.2 mm long, bases rounded, appendages rotund-acute; styles 2.2-2.7 mm long, branches slightly recurved, flattened, minutely pubescent below and along the margin; ray achenes 1.5-1.8 mm long, black, striate, obconical, with 3-4 obscure ridges, laterally compressed, glabrous, epappose; disc achenes 1.5-1.8 mm long, obconical, with 4-5 obscure ridges, black, striate; pappus, when present, of 14-20 lanceolate-linear ciliate awns, composed of alternating short awns (1.0-1.5 mm long) and long awns (2-2.2 mm long), glabrous when epappose and hirtellous when pappose; chromosome number $n = 8$.

ECOLOGY AND DISTRIBUTION. In open pine woods often on limestone ridges and stream margins at elevations from 3140 to 3500 meters. Occasional in occurrence; flowering from July through December. Endemic to the Sierra de los Cuchumatanes of Guatemala (Fig. 5).

SPECIMENS EXAMINED. GUATEMALA. HUEHUETENANGO: Sierra de los Cuchumatanes, at Km 311 on Ruta Nacional 9 N, elev ca 3360 m, 2 Aug 1959, Beaman 3010 (MSC); Sierra de los Cuchumatanes, between Kms 324 and 325 on Ruta Nacional 9 N, 4 Aug 1959, Beaman 3032 (MSC); Sierra de los Cuchumatanes, between Tojiah and Chemal at Km 317.5 on Ruta Nacional 9 N, elev ca 3400 m, 30 July 1960, Beaman 3801 (MSC); Sierra de los Cuchumatanes, between Tojiah and San Juan Ixcoy at Km

3245 on Ruta Nacional 9 N, elev ca 3140 m, 31 July 1960, Beaman 3846 (MSC); Sierra de los Cuchumatanes about 28 miles from Huehuetenango, slopes of Cerro Chemal, elev 3350 m, 30 Oct 1958, Hawkes, Hjerting & Lester 1764 (F); Sierra de los Cuchumatanes, on Ruta Nacional 9 N at Km 311, 26 Aug 1961, Longpre 226 (MSC); Sierra de los Cuchumatanes on Ruta Nacional 9 N between Km 317.5 and 319 km, 26 Aug 1961, Longpre 227 (MSC); Sierra Cuchumatanes, elev 10400 ft, 14 Sept 1934, Skutch 1234 (GH, holotype; F, US); along road in region of Chemal, Sierra de los Cuchumatanes at km 36, elev ca 3300 m, 31 Dec 1960, Standley 81685 (F); near Tunima, Sierra de los Cuchumatanes, elev 3300-3500 m, 6 July 1942, Steyermark 48290 (F, US); alpine areas in vicinity of Tunima, Sierra de los Cuchumatanes, elev 3400-3500 m, 7 July 1942, Steyermark 48345 (US).

As in Sabazia humilis and S. multiradiata, epappose and pappose forms are found within the same population, Blake (1937) described the pappose individuals as S. pinetorum var. dispar. In view of the inconsistent nature of this characteristic, I do not consider it worthy of taxonomic recognition.

Sabazia pinetorum is allied to S. mullerae, but differs in having narrower petiolate leaves, slender peduncles, smaller heads, shorter disc corollas, styles and achenes, epappose ray achenes only, and pappus awns which are generally half as long. Although somewhat more distantly related,

S. trianae is similar in possessing elliptic-lanceolate leaves, terminal and solitary heads, a two-seriate involucre, and unequal, linear-lanceolate awns.

6. Sabazia leavenworthii Longpre, sp. nov.

Type. MEXICO. MICHOACAN: Tancitaro, along trail on eastern slope of mtn in open areas among grasses, 13 Aug 1961, E. K. Longpre 105 (MSC, holotype!).

Planta perennis, decumbens usque ascendens, 12-33 cm alta, systematibus fibrosis radicum (interdum rhizomate brevi minute); caules pilosi usque dense villosi-pilosi; folia opposita, ovata, elliptica-ovata vel triangulata-ovata, basibus obtusis, cuneatis vel truncatis, apicibus acutatis, 1.1-3.9 (-5) cm longa, 0.4-2.7 (-3.5) cm lata, longitudo minus quam bis latitudo, remote usque dense pilosa, strigosa-pilosa vel sericea-pilosa supra et infra, petioli 2 mm (in foliis superis lanceolatis) -7 mm longi, crassi, dense villosi-pilosi, margine crenato-serrato, 2-5 paribus dentium, remotorum non profundorum; capitula 1-6, solitaria, terminatrica vel axillaria, 2.5 cm lata (includentia radii); paleae ellipticae-lanceolatae, acuminatae, lobis 1 vel 2 lateralibus, 4.5-5.5 mm longae; involucrum 2-3 seriebus, 10 mm latum, 5 mm altum; 8 radii flosculi, albi supra, rosei-purpurei infra, tubi 1-2 mm longi, sparsim hirti, ligulis oblongis-

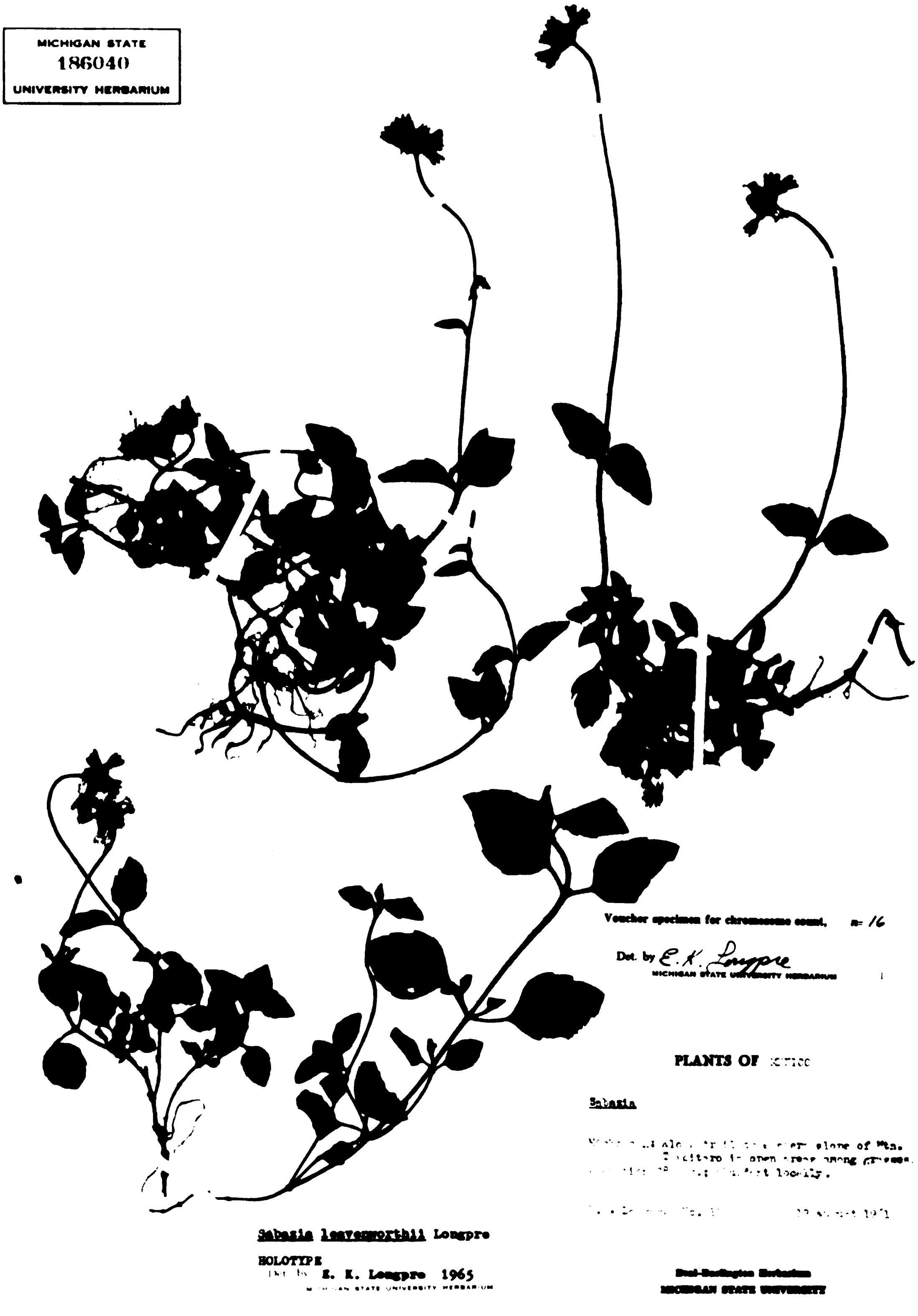
ovatis usque subquadratis, 7.8-10 mm longis, 5-6.3 mm latis, 3 lobis apicalibus, obtusis, 1-2 mm longis; disci flosculi circa 50-55, infundibuliformes, tubi 0.7-1 mm longi, sparsim hirti, limbis 2 mm longis, basi styli circumdati nectario; radii achenia obovata, 3-4 obscuris porcatis, lateraliter compressis, 1.8-2 mm longis, glabella, sine pappo; disci achenia tenuiter obconica, 1.5-2.5 mm longa, omnino strigosa-hispida, sine pappo; chromosomatum numerus n = 16.

Perennial, decumbent to ascending, 12-33 cm tall, from a fibrous root system, sometimes with a short, minute rhizome; stems pilose to densely villous-pilose, striate; peduncles 2-13.5 cm long, densely pilose; leaves opposite, ovate, elliptic-ovate or triangular-ovate, bases obtuse, cuneate or truncate, apices acute, upper leaves lanceolate, 1.1-5 cm long, 0.4-3.5 cm wide, less than twice as long as wide, remotely to densely pilose, strigose-pilose, or sericeous-pilose above and below, petioles 2 mm (on upper lanceolate leaves) -7 mm long, stout, densely villous-pilose, margins crenate-serrate, with 2-5 pairs of remote, shallow, gland-tipped teeth; heads 1-6 per plant, solitary, terminal or axillary, 2.5 cm wide (including rays); pales elliptic-lanceolate, with 1 or 2 lateral lobes, acuminate, 4.5-5.5 mm long; involucre in 2-3 series, 10 mm wide, 5 mm high; outer phyllaries elliptic-ovate or ovate, obtuse, 4.5-6 mm long, 2-3 mm wide, glabrous, entire to very sparsely ciliate-

subglandular, herbaceous, often purple colored along the margins and apices, striate, 7-10 nerved; middle phyllaries similar to the outer but somewhat longer and broader, 7 mm long and 3.2 mm wide; inner phyllaries elliptic-lanceolate or oblong-lanceolate, 6-7 mm long, 2-3 mm wide, sometimes laciniate-ciliate and subglandular at the apices, membranaceous; ray florets 8, white above, roseate-purple below, tube 1-2 mm long, sparsely hirtellous, ligule oblong-obovate to subquadrate, 7.8-10 mm long, 5-6.3 mm wide, obtusely 3-lobed, 1-2 mm long, styles 2.2-3 mm long, the branches acute, flattened; disc florets ca 50-55, funnelform, tube 0.7-1 mm long, sparsely hirtellous, limb 2 mm long, styles 2.7-3.3 mm long, apices subulate, nectary enclosing the base of the style; anthers 1-1.3 mm long, subsagittate, appendiculate; ray achenes obovate in outline, obscurely 3-4-ridged, laterally compressed, 1.8-2 mm long, glabrous, epappose; disc achenes slenderly obconical, 1.5-2.5 mm long, entirely strigose-hispidulous, epappose; chromosome number $\underline{n}$ = 16. Plate 5.

ECOLOGY AND DISTRIBUTION. In open fir and pine forests, under the partial shade of alders, and in subalpine open grassy areas at about 3100 to 3150 meters. Collected in flower from August through October. Apparently endemic to the mountains of Michoacan (Fig. 5).

Plate 5. Photograph of the holotype of Sabazia leavenworthii.


MICHIGAN STATE
186040
UNIVERSITY HERBARIUM
Voucher specimen for chromosome count, n= 16
Det. by E. K. Longpre
MICHIGAN STATE UNIVERSITY HERBARIUM
PLANTS OF
Sabazia
Sabazia leavenworthii Longpre
HOLOTYPE
E. K. Longpre 1965
MICHIGAN STATE UNIVERSITY HERBARIUM
MICHIGAN STATE UNIVERSITY

SPECIMENS EXAMINED. MEXICO. MICHOACAN: Southwest side of Cerro San Andres, ca 12 kms north of Ciudad Hidalgo, elev 3100 m, 6 Sept 1960, Beaman 4242 (MSC); Tancitaro, elev 3150 m, 14 Oct 1940, Hinton 15526 (GH, TEX, US); Tancitaro, along trail on eastern slope of mtn in open areas among grasses, 13 Aug 1961, Longpre 105 (MSC, holotype).

Sabazia leavenworthii is named for William C. Leavenworth who, as a Ph.D. candidate in Botany, obtained many important collections from southwestern Michoacan and prepared a study of the vegetation of the region between Cerro Tancitaro and the Rio Tepalcatepec (Leavenworth, 1946). He was killed in action in France, October 29, 1944.

This species is closely allied to S. multiradiata and S. sarmentosa and has several characters in common with both. In view of this fact, it is possible that S. sarmentosa, with n = 24, could have originated as an allopolyploid from the ancestors of S. leavenworthii (n = 16) and S. multiradiata (n = 8). Populations of the three species are found within approximately a 280 mile radius of each other. Sabazia multiradiata differs from S. leavenworthii in possessing sessile (rarely subsessile) leaves, stems with soft, appressed trichomes, a 3- to 4-seriate involucre and often the heads are in loose subcyme. Sabazia sarmentosa is distinguished from S. leavenworthii in being procumbent or decumbent (rarely ascending or erect), having disc achenes which are glabrous

or sparsely strigose-hispidulous along the margins, often having adventitious roots at the lower nodes, and with acuminate leaf apices.

7. Sabazia sarmentosa Less.

Plants perennial, trailing, procumbent or decumbent, ascending (rarely erect), up to 90 cm, with fibrous roots; stems simple or subsimple, branching from the axils, glabrous below to lightly pilose or moderately strigose-pilose above, striate, greenish or greenish-purple, often with adventitious roots from the lower nodes, rarely from the upper nodes, leaves opposite, sometimes subdecussate, ovate, elliptic-ovate, triangular, elliptic-lenceolate to lanceolate, bases cuneate, obtuse to truncate, apices acuminate or rarely acute, serrate or crenate-serrate, ciliate, up to 6.5 (-8.5) cm long, up to 4 (-6.8) cm wide, 3-5 nerved with secondary reticulate venation, very sparsely strigose-pilose to densely strigose above, the trichomes with subtuberculate bases; petioles often winged, glabrous to strigose-hispidulous, often with black glandular-capitate trichomes; peduncles up to 20.5 cm long, with densely appressed whitish trichomes near the heads, these sometimes intermixed with glandular-capitate trichomes; heads 1 to 8, terminal or axillary, sometimes in a loose subcyme, hemispherical to suboval, 1-2.5 cm wide (including rays); receptacle convex to subconical, paleaceous;

pales persistent, elliptic-lanceolate, acuminate, scarious, entire or with 2-3 ciliated acuminate lobes; involucre in 2-3 subequal series, 4.5-10 mm wide, 4-6 mm high; outer phyllaries elliptic-ovate or lanceolate-ovate, obtuse, sometimes sparsely subciliate at the apex, herbaceous, 3-6 mm long, 1.2-3 (-4) mm wide; innermost phyllaries longer than the outer, elliptic-ovate to oblong-lanceolate, 3-10 mm long, 0.5-3.5 mm wide, acute to acuminate, scarious or hyaline, glabrous, apical margins usually minutely laciniate; ray florets 5-11, white above, white or roseate below, tube (0.5-) 1-2 mm long, glabrous to hirtellous, ligules cuneate-obovate to subquadrate, 4.8-10 mm long, (2.5-) 3-7 mm wide, with 3 apical obtuse or acute lobes, 1-3.5 mm long, style 1.5-3.5 mm long, branches oblique or recurved, apices subulate or flattened-ovate; disc florets yellow, 30-65 (-100), funnelform to broadly tubular, tube 0.5-1 mm long, sparsely pilose or strigose-hirtellous, limb 1-2.3 mm long; anthers 0.8-1.5 (-2) mm long, subsagittate, appendiculate; styles 2-3.5 mm long, oblique or recurved, acute or with a subulate apex, nectary usually enclosing the base of the style; ray achenes narrowly but somewhat laterally compressed, obconical, obscurely 3-4 ridged, epappose or pappose, with 12-16 spinulose, fimbriate scales or sublanceolate awns, glabrous or minutely strigose along margins (seldom over the entire achene surface); disc achenes obovate or obconical, 1-2 (-2.5) mm long, obscurely 4-ridged, glabrous, hispidulous or more commonly

minutely strigose along the margins only, epappose or pappose, pappus, when present, like that of the ray achenes, 1/3 to 2/3 the length of the corolla, scarious.

Key to the varieties

A. Plants with small (1.1-2.5 cm long) elliptic-lanceolate leaves, light green on both surfaces; both ray and disc achenes pappose . . . . . 7c. var. lancifolia

AA. Plants with larger (1-6.5 cm long) triangular, ovate, elliptic-ovate or sometimes lanceolate leaves, darker green on the upper surface, ray achenes epappose, disc achenes epappose or pappose . . . . . B.

B. Achenes pubescent over their entire surface; ligule tubes sparsely pubescent; leaves triangular or ovate, bases truncate or obtuse; plants of Costa Rica and Panama. . . . . 7b. var. triangularis

BB. Achenes glabrous to sparsely strigose-hispidulous along the margins; ligule tubes moderately to densely pubescent; leaves ovate, elliptic-ovate or lanceolate; plants of Mexico and Guatemala . . . . . 7a. var. sarmentosa

7a. Sabazia sarmentosa Less. var. sarmentosa

Sabazia sarmentosa Less. Linnaea 5: 148. 1830. Baziasa sarmentosa Steudel, Nom. ed. 2. 1: 192. 1840. Type. MEXICO. VERACRUZ: "Serro Colorado", Aug 1828,

Schiede 296 (HAL, holotype, MSC photos 3895I, 3895II!; GH, tracing and fragment, isotype!).

Allocarpus sabazioides Schlecht. Linnaea 9: 590. 1834. Calea sabazioides (Schlecht.) Hemsl. Biol. Centr. Am. Bot. 2: 206. 1881. Type. MEXICO. VERACRUZ: Near San Miguel del Solado and La Joya, June 1829, Schiede (HAL, holotype; MSC photos 3895I, 3895II!).

Tridax ehrenbergii Sch.-Bip. ex Klatt, Leopoldina 23: 145. 1887. Type. MEXICO. OAXACA: Chinantla, July 1841, Liebmann 598 (C, holotype; MSC photo 4663!).

Sabazia radicans Blake, Contrib. U.S. Nat. Herb. 22: 615. 1924. Type. MEXICO. PUEBLA: Honey, near Trinidad Iron Works, on wet banks, 11 July 1904, Pringle 8943 (US, holotype!; GH, MO, MSC, NY, UC, isotypes).

Plants (6-) 21-86 cm long; leaves ovate, lanceolate-ovate or elliptic, bases cuneate to obtuse, 1-6.5 cm long, 0.3-4 (-6.8) cm wide, margins with (2-) 3-8 (-9) mammose teeth; ray florets 5-11, generally 8; disc florets ca 35-65 (-100); ray achenes glabrous or minutely strigose along the margins, seldom pubescent over entire achenial surface, epappose or rarely pappose, the pappus, when present, with 12 spinulose fimbriate scales 0.8 mm long; disc achenes glabrous, hispidulous over the entire achenial surface or more commonly minutely strigose-pilose along the margins only, usually epappose but sometimes with spinulose or spa-

tulate, fimbriate and minutely laciniate scales 0.5-2 mm long, 1/3 to 2/3 the length of the corolla; chromosome number n = 24.

ECOLOGY AND DISTRIBUTION. Usually in humid habitats such as along stream banks and in cloud forests, although two collections were found growing in volcanic ash on Volcan Atitlan in Guatemala. At elevations ranging from 1930 meters to around 3550 meters. Apparently in flower every month of the year in some part of the range. Rooting at the nodes above the ground was observed occasionally in herbarium specimens of var. sarmentosa and var. triangularis. This seems to be largely due to environmentally elicited responses since this character is exhibited sporadically in about half of the collections from Mexico, Guatemala, and Panama. Collections from very moist or humid habitats (Longpre 257, Longpre 474, Pringle 8943, and Steyermark 43446) typically had adventitious roots. Other collections with this character lack the necessary habitat data to confirm whether or not the presence of adventitious roots are correlated with a moist environment. Experimental studies also appear to support this phenomenon, for living specimens of var. sarmentosa (Longpre 257 and Longpre 474) when cultivated in a non-shaded and relatively dry greenhouse never produced exposed roots along the nodes. In most cases, collections coming from mesic or (in rare cases) semi-dry areas are

without the adventitious roots. Ranging from the Sierra Madre Oriental (northern Veracruz) across the transvolcanic belt to the Sierra Madre del Sur (western Guerrero) and southward into the mountains of Guatemala (Fig. 4).

SPECIMENS EXAMINED. MEXICO. CHIAPAS: Near San Cristobal, elev 7000-8800 ft, 18 Sept 1895, Nelson 3232 (GH, US). GUERRERO: Paracho, distr. Mina, elev 3280 m, 1 Dec 1936, Hinton 9944 (NY, UC). OAXACA: NW slope Mt. Zempoaltepec, 8000 to 10000 ft, 10 July 1894, Nelson 680 (GH, US). PUEBLA: Boca del Monte, 16-19 Nov 1907, Arsène 2134 (US); Honey, 4 Sept 1961, Longpre 474 (MSC); Honey, along wet stream bank east of train station, 2 Aug 1962, Longpre 502 (MSC); Honey, elev 5800 ft, 11 July 1904, Pringle 8943 (US, holotype of S. radicans; GH, MO, MSC, NY, UC). VERACRUZ: San Miguel, elev 6600 ft, 3 June 1938, Balls B4699 (UC, US); "Serro Colorado", August, 1828, Schiede 296 (GH, isotype). GUATEMALA. CHIMALTENANGO: Volcan Acatenango, north side of mtn, elev ca 3620 m, 6 Aug 1960, Beaman 4044 (MSC); Sta. Elena, Tecpam, 5 Dec 1936, Johnston 410 (F, GH); Chichavac, Nov-Dec 1930, Skutch 68 (US); Chichavac, 23 July 1933, Skutch 498 (US); Chichavac, 5 Dec 1933, Skutch 749 (US); Cerro de Tecpam, region of Santa Elena, elev 2400-2700 m, 26 Dec 1938, Standley 61060 (F). EL PROGRESO: between Calera & summit of Volcan Siglo, elev 2000-3300 m, 21 Jan 1942, Steyermark 43063 (F, GH, US); Sierra de Las Minas,

hills between Finca Piamonte, elev 2400-2500 m, 4 Feb 1942, Steyermark 43446 (F). HUEHUETENANGO: Sierra de los Cuchumatanes, between Tojiah & San Juan Ixcoy, 31 July 1960, Beaman 3847 (MSC); Sierra de los Cuchumatanes, along Ruta Nacional 9 N between Km 326 and 327, 26 Aug 1961, Longpre 257 (MSC); above San Juan Ixcoy, Sierra de los Cuchumatanes, 4 Aug 1942, Steyermark 50105 (F). QUEZALTENANGO: Volcan Santo Tomas, elev 2500-3700 m, 22 Jan 1940, Steyermark 34811 (F). SAN MARCOS: Volcan Tajumulco between Las Canojas & top of ridge, 7 mi from San Sebastian, elev 3300-3900 m, 16 Feb 1940, Steyermark 35893 (F, GH). SACATEPEQUEZ: Volcan de Agua, 12 Nov 1936, Johnston 204 (F, NY); Volcan de Agua, 23 July 1937, Johnston 812 (F, GH, NY); Volcano Agua, 4 Feb 1908, Kellerman 7190 (F); Volcan de Agua, elev 3150-3300 m, 22 March 1905, Maxon & Hay 3691 (US); slopes of Volcan de Agua, above Santa Maria de Jesus, elev 2250-3000 m, 11 Feb 1939, Standley 65205 (F, NY). SOLOLA: Volcan Atitlan, near summit of mtn, elev 3535, 10 Aug 1960, Beaman 4058 (MSC); Volcan Atitlan, south facing slopes, elev 8300 ft, 11 June 1942, Steyermark 47438 (F, US). TOTONICAPAN: ca 10 kms east of Totonicapan on Ruta Nacional No. 1, 3 Aug 1960, Beaman 3981 (MSC); 9 kms east of Totonicapan on Ruta Nacional No. 1, 3 Aug 1960, Beaman 3982 (MSC).

Var. sarmentosa is usually found in humid habitats such as along wet stream banks. It is wide spread in its

distribution ranging north to Puebal, west to Guerrero, east to Veracruz, and south to the mountains in Guatemala. It appears to flower in every month of the year. Rooting at the nodes above the ground was occasionally observed in herbarium specimens of var. sarmentosa and var. triangularis. This seems to be largely due to environmentally-elicited responses since this character is exhibited sporadically in about half of the collections from Mexico, Guatemala, and Panama. Collections from very moist or humid habitats (Longpre 257, Longpre 474, Pringle 8943, and Steyermark 43446) typically had adventitious roots. Other collections with this character lack the necessary habitat data to confirm whether or not the presence of adventitious roots are correlated with a moist environment. Experimental studies also appear to support the idea that there is a correlation, for living specimens of var. sarmentosa (Longpre 257 and Longpre 474) when cultivated in a non-shaded and relatively dry greenhouse never produced exposed roots along the nodes. In most cases, collections coming from mesic or (in rare cases) semi-dry areas are without these adventitious roots.

The type specimens of Sabazia sarmentosa and Allocarpus sabazioides in H are mixed on the same sheet without indication as to which label applies to which specimen. The photograph (MSC 3895 I, & 3895 II) shows the specimens to be almost identical in all superficial details. Since

Allocarpus sabazioides was distinguished by Schlechtendal almost exclusively on the basis of a pappus being present, I feel confident in referring this species to the synonymy of S. sarmentosa.

With respect to var. sarmentosa, Blake distinguished two species and two varieties differing in leaf morphology and achenial pubescence or stem pubescence. He considered Sabazia radicans to have glabrous stems and hispidulous disc achenes. These characters, however, were not found to be consistent.

Some collections (Beaman 4044 and Maxon & Hay 3691) are unusual in having densely strigose-pilose pubescence on the upper and lower leaf surfaces. This difference in leaf morphology appears to be related to habitat. These collections were found in open disturbed soil or in volcanic ash. In other characters they agree with more typical var. sarmentosa. The pubescent forms mentioned above appear to be very similar to Sabazia leavenworthii. However, this species can be distinguished by its decumbent to ascending habit, longer leaves, disc achenes pubescent over the entire surface, and slightly longer ligule tubes. The small-leaved forms of var. sarmentosa, because of their pappose and pubescent achenes, were formerly recognized as Calea sabazioides.

7b. *Sabazia sarmentosa* Less. var. *triangularis* (Blake) Longpre, comb. nov.

Sabazia triangularis Blake, Proc. Amer. Acad. 22: 615. 1924. Type. PANAMA. CHIRIQUI: Around El Potrero Camp, Chiriqui Volcano, elev 2800-3000 m, 10 to 13 March 1911, *H. Pittier 3109* (US, holotype!).

Sabazia triangularis var. *papposa* Blake, Ann. Mo. Bot. Gard. 26: 317. 1939. Type. PANAMA. CHIRIQUI: Loma Larga to summit, Volcan de Chiriqui, elev ca 2500-3380 m, 4-6 July 1938, *Woodson, Allen & Seibert 1055* (US, holotype!; GH, NY, isotypes).

Plants 20-90 cm tall, procumbent or decumbent; leaves triangular-ovate to ovate, bases truncate or obtuse, apices acuminate, 1.2-5 (-8.5) cm long, 0.4-2.5 (-4.5) cm wide, serrate with 4-15 pairs of ascending mammose teeth; ray florets 5; disc florets ca 30; ray achenes epappose; disc achenes epappose or pappose, pappus, if present, of 6-8 oblong-spatulate scales, fimbriate-ciliate at the apex, 0.8 mm long.

ECOLOGY AND DISTRIBUTION. Along streams, humid ravines and in cloud forests, from about 2500 to 3500 meters. Collected in flower from January to July. Endemic to the Cordillera de Talamanca in Costa Rica and Volcan Chiriqui in Panama (Fig. 4).

SPECIMENS EXAMINED. COSTA RICA: Cartago, 28 April 1946, Pacheco 78 (F) PANAMA. CHIRIQUI: Bajo, Boquete, 25 Jan 1938, Davidson 202 (GH, US); Potrero Muleto, Volcan de Chiriqui, Boquete, elev 10,400 ft, Davidson 1010 (DS, GH, US); around Potrero Camp, Chiriqui Volcano, elev 2800-3000 m, 10-13 March 1911, Pittier 3109 (US, holotype); Loma Larga to summit, Volcan Chiriqui, elev ca 2500-3380 m, 4-6 July 1938, Woodson, Allen & Seibert 1055 (GH, NY, US).

Although Blake (1924) recognized the taxon as a species, it differs in no significant way from variety sarmentosa outside the fact that it tends to have truncate leaf bases or a triangular-ovate leaf shape, sparsely pubescent ligule tubes, and achenes which are pubescent over their entire surface. Blake (1939) recognized a pappose form of S. triangularis as var. papposa. This sporadic occurrence of the pappus is also common in Sabazia multiradiata, S. pinetorum and S. humilis. In view of the fact that Blake's species and var. of S. triangularis are found on the same mountain at approximately the same elevations, I regard the pappose individuals as forms of the var. triangularis.

7c. Sabazia sarmentosa Less. var. lancifolia Longpre, var. nov.

Type. MEXICO. HIDALGO: Vicinity of Molango on road to Lolotla, wet banks by road, elev 1650 m, 9 Nov 1946, H. E. Moore Jr. 1989 (GH, holotype!; UC, US, isotypes).

Plantae perennes, systemate radicum fibrosarum, caules simplices vel parvi-ramosi, usque 46 cm altae; folia elliptica-lanceolata, 1.1-2.5 cm longa, 0.3-0.6 cm lata, moderate pilosa-striogosa, subviridia supra et infra, ciliata; petioli 1-2.5 mm longi, strigosi-hispidi; pedunculi 5.5-16.5 cm longi; capitula usque 8, subcyma laxa, terminalies et axillares, 1.3-1.5 cm lata (includentia radii); receptaculum paleis linearis 2.3-3 mm longis, integris, interdum trilobatis; involucrum campanulatum 8 mm latum, 4 mm altum; 8 flosculi radii, ligulis quadratis-ovatis, 4.8 mm longis, 3.5 latis, 3 lobis acutis, 1.3-1.8 mm altis; flosculi disci circa 40, tubis 1 mm longis, pilosis, corollis infundibuliformis, limbis 1-2 mm longis, ramis stylis subulatis, puberulis apice extra; achenia (immatura) radii et disci, gracilia obconica, quadriporcata, 1 mm longa, minute strigosa secus juga, pappo, 16 aristis sublanceolatis, acutis, laciniatis, et longitudinis inaequalis.

Plants up to 46 cm long, simple or branched; leaves elliptic-lanceolate, 1.1-2.5 cm long, 0.3-0.6 cm wide, light

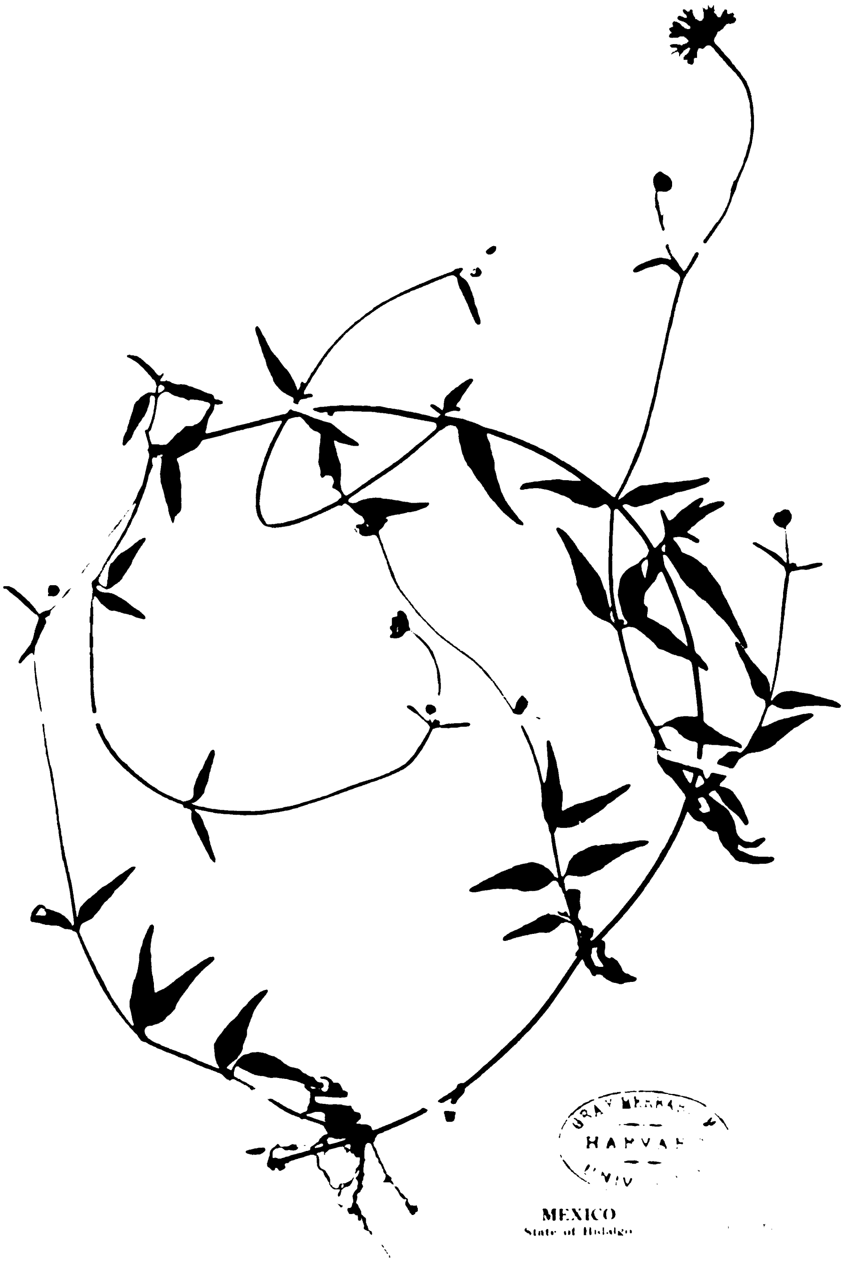
green above and below, margins ciliate; heads up to 8 per plant, terminal and axillary, hemispherical, 1.3-1.5 cm wide (including the rays); ray florets 8, white above, white or roseate below, ligule quadrate-obovate, 4.8 mm long, 3.5 mm wide, with acute lobes, 1.3-1.8 mm high; disc florets ca 40, corolla funnelform, limb 1-2 mm long; both the ray and disc achenes (immature) slenderly obconical, 4-ridged, 1 mm long, minutely strigose along the ridges, pappus present on ray and disc achenes, of 16 sublanceolate awns, acute, laciniate, unequal in length. Plate 6.

ECOLOGY AND DISTRIBUTION. See data cited for the type collection. Figure 4.

SPECIMENS EXAMINED. Known only from the type collection.

Variety lancifolia is similar to the small leafed form of var. sarmentosa, but differs in possessing axillary heads, lighter green leaves, subquadrate ray ligules, and pappose ray achenes. It may also be related to Sabazia pinetorum which likewise has small, elliptical-lanceolate or oblong-lanceolate (but somewhat smaller) leaves. In addition, S. pinetorum has similar, unequal pappus awns. It is distinguished, however, by the very prominent foliar midveins, darker green leaves, and a decumbent habit. The present distributions of var. lancifolia and S. pinetorum might be interpreted as having originally evolved as a distinct, narrow leafed population from the S. sarmentosa complex.

Plate 6. Photograph of the holotype of *Sabazia sarmentosa* var. *lancifolia*.



MEXICO
State of Hidalgo

... ntosa v r. l ncifoli longpre

HOLOTYPE

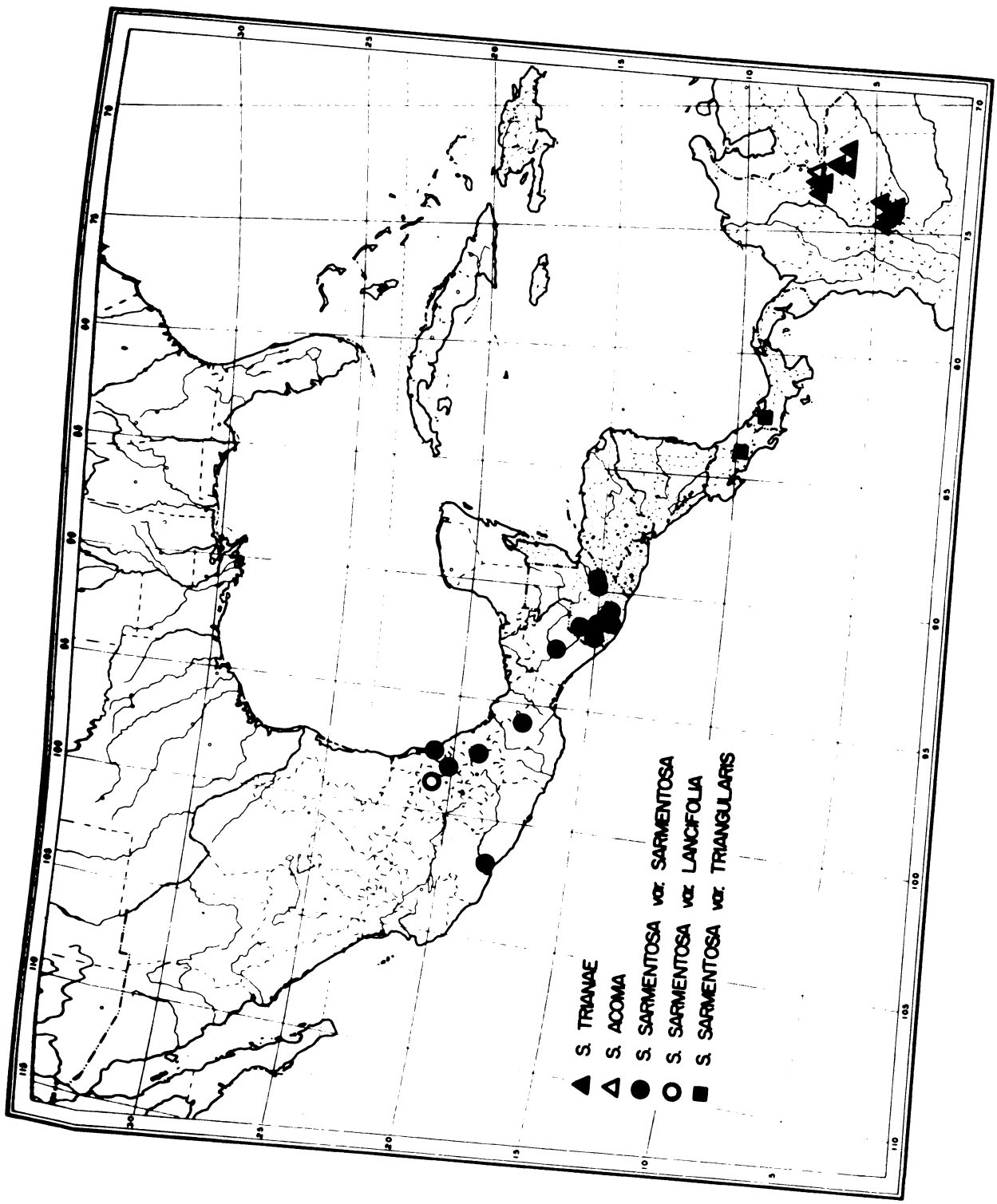
Det. by E. K. Longpre 196?

MICHIGAN STATE UNIVERSITY HERBARIUM

District: Molango

H. E. Moore, Jr. No. 1...

Figure 4. Geographical distribution of S. trianae, S. acoma, S. sarmentosa var. sarmentosa, S. sarmentosa var. triangularis, and S. sarmentosa var. lancifolia.


S. TRIANAE
S. ACOMA
S. SARMENTOSA var. SARMENTOSA
S. SARMENTOSA var. LANCIFOLIA
S. SARMENTOSA var. TRIANGULARIS

8. Sabazia liebmannii Klatt

Key to the varieties

A. Leaves subcoriaceous, acuminate, with prominent whitish midrib on lower surface; outer phyllaries strongly scarious-margined. . . . . 8b. var. hintonii

AA. Leaves not subcoriaceous, acute, midrib (although larger) no more prominent than the two laterals; outer phyllary margin generally herbaceous . . . . . B.

B. Leaves with prominent reticulate secondary venation underneath, densely pilose-strigose to hirsute above, subcanescent to densely strigose below; peduncles usually with glandular capitate trichomes intermixed with the dense hirsute to pilose-strigose trichomes near the apex; outer phyllaries pilose-strigose, ciliate; pales entire (never lobed), ray corolla tubes 2.3-3 mm long. . . . . 8d. var. michoacana

BB. Leaves without prominent reticulate secondary venation underneath; peduncles without glandular-capitate trichomes; outer phyllaries usually glabrous; pales usually trilobed (sometimes bilobed or entire); ray corolla tubes 1-2 mm long. . . . . C.

C. Leaves elliptic to elliptic-ovate, lamina length more than twice the width, base cuneate, sparsely to moderately strigose above; stems often reddish-purple, glabrous to sparsely strigose-pilose (sometimes moderately

so). . . . . 8a. var. liebmannii

CC. Leaves ovate to elliptic-ovate, lamina length less than twice the width, obtuse or cuneate, densely strigose to scabrescent above; stems often yellowish-green, densely hirsute to strigose. . . 8c. var. ovatifolia

8a. Sabazia liebmannii Klatt var. liebmannii

Sabazia liebmannii Klatt, Leopoldina 23: 90. 1887. Tridax liebmannii Sch. Bip. ex Klatt (pro syn.) nom. nud. Type. MEXICO. OAXACA: Pelado, August 1842, Liebmann 694 (C, holotype; MSC photo 4672!; US, fragment!).

Perennial plants from lignescent erect or oblique rhizomes with fibrous lateral roots, 29-38 cm tall; stems erect, simple or branching from the base, glabrous to sparsely strigose-pilose, striate, often reddish-purple; leaves opposite, petiolate to subsessile, the petioles (0.5-) 1-6 mm long, elliptic to elliptic-ovate, the upper leaves usually lanceolate-ovate, the lamina 1-5.7 cm long, 0.5-2.5 cm wide, the margins serrate or sometimes serrate-dentate with (2-) 3-4 (-5) pairs of remote, callous-tipped teeth, ciliate, apices acute, bases cuneate (rarely obtuse), sparsely to moderately strigose above (sometimes glabrate), glabrous to densely strigose-pilose below, usually more densely so along the veins, lighter green and often purplish underneath; peduncles (3.5-) 9-19 (-21) cm long, with pubescence similar

to the stem but whitish and more appressed, especially near the heads; heads terminal, solitary or in a loose cymose inflorescence, often subtended by a single bract; involucre ovoid to campanulate, 4-7 (-12) mm high and 7-13 mm wide, phyllaries imbricate, 3 (-4)-seriate, distinct to the base, the outer and middle ovate (rarely oblong-ovate) to broadly ovate, purple tinged along the upper margins and apices, 3-7.5 mm long, (1.5-) 2-4 mm wide, acute to obtuse, herbaceous but with narrow membranaceous margins, with 8-10 prominent nerves, often carinate near the base, glabrous (rarely strigose), the apices minutely ciliate-fimbriate; inner phyllaries membranaceous, narrowly ovate, about as long as the outer, 2 mm across and 2 mm high; pales persistent, elliptic-lanceolate, scarious, glabrous, 3-6 mm long, 0.4-1 mm wide, attenuate or acuminate, trifid (sometimes bifid or unlobed), the lateral lobes 1/4 to 1/2 as long as the middle one; ray florets 5-13 (usually 8), pistillate and fertile, tubular at the base for 1.3-2 (-2.5) mm, densely pilose, ligules obliquely ascending to perpendicular to the involucre, white above, usually roseate-purple below, (3.4-) 6-11 (-14) mm long and (2-) 4-6 (-8) mm wide, oblong-obovate or oblong, sometimes quadrate, apices with 3 acute to obtuse lobes (0.5-) 1-3.8 mm long and 1.2 mm wide, style branches tapering to a point; disc florets 30-65, yellow, perfect, funnelform to broadly tubular, tube (0.6-) 1-1.5 mm long, densely pilose, the limb (1.5-) 2-2.8 (-3.5) mm long, 0.6-1 mm wide, sometimes

minutely strigose along the margins, with 5 acute lobes, papillate on the inside, minutely pubescent on the outside, anthers 1-1.8 mm long, with acute, apical appendages, and subsagittate bases; style branches usually recurved, tapering to a subulate apex, pubescent on the outside and inside; achenes of disc and ray florets similar, black, striate, obovate in outline, obscurely 3-4-ridged or slightly flattened, those near the periphery incurved, glabrous or rarely sparsely puberulent near the apex and along the ridges, (1.3-) 2-2.3 (-2.6) mm long; pappus absent; chromosome number, n = 24.

ECOLOGY AND DISTRIBUTION. Usually found in disturbed or eroded areas of reddish clay loam or brown sandy loam along roadsides, in rocky crevices, and under partial shade of open oak-pine forests at elevations of 1800 to 3100 meters. Locally abundant. Flowering mostly from July to October (less often in January and February). Restricted to the uplands of the Sierra Madre del Sur in Oaxaca and Puebla (Fig. 6).

SPECIMENS EXAMINED: MEXICO. GUERRERO: Alrededores de la problacion, Omiltemi, 20 km al W. de Chilpancingo, 2,250 m, 1 Sept 1962, Rzedowski 15953 (MSC). OAXACA: On the Oaxaca-Valle Nacional highway 25 miles W of Ixtlan, elev ca 2550 m, 21 July 1960, Beaman 3661 (MSC); Cerro de San Felipe, elev 1800 m, 25 July 1897, Conzatti & Gonzalez

395 (GH); Cerro San Felipe, Distrito del Centro, elev 2500 m, 18 Oct 1908, Conzatti 2267 (F); 48 road miles N of Oaxaca & 17 road miles south of pass between Oaxaca & Tuxtepec, elev 9300 ft, 12 Oct 1962, Cronquist 9654 (MSC, NY); Pan-Am Hwy (Km 493-494) 5-1/2 Km SE of La Rangerie de Tejocote, ca 2100 m, 24 Aug 1960, Iltis et al. 1275 (TEX); Mtns along route 190 ca 29 miles NW of Oaxaca, 27 July 1960, King 3524 (DS, TEX, US); Along hwy 175 (Valle Nacional) between Km 213 & 212 (12.5 miles from hwy 190), elev 2500 m, 30 Aug 1961, Longpre 292 (MSC); along hwy 190 between Km 499 & 498, 29.7 miles north of Oaxaca, 30 Aug 1961, Longpre 293 (MSC); Vicinity of Cerro San Felipe, 1894, Nelson 1126 (GH, US); along route 175 toward Ixtlan, 14 Aug 1961, Powell & Edmondson 674 (TEX); Along route 190, 25 miles west of Oaxaca, 15 Aug 1961, Powell & Edmonson 706 (TEX); Sierra de San Felipe, elev 10,000 ft, 25 Sept 1894, Smith 288 (F, MO, US). PUEBLA: Cerro Verde, in the vicinity of San Luis Tultitlanapa, Puebla, near Oaxaca, July 1908, Purpus 3110 in part (F 2 sheets, GH, NY, UC, US).

Variation, chiefly in leaf morphology, is attributed to hybridization as evidenced by collections with intermediate leaf characters of S. liebmannii var. liebmannii and var. ovatifolia. The possibility of natural hybridization is further suggested by experimental crosses (Longpre 292 and Longpre 199) which were successfully carried out between

these two varieties; both have the same chromosome number, n = 24.

In their revision of Sabazia, Robinson and Greenman (1904) established a new variety of S. liebmannii, var. heterocarpa based on one of two plants mounted together from Seaton's collection 167. One is epappose and the other has a disc pappus. At the time of the above revision, only four species which are recognized as Sabazias today were known. In addition, Robinson and Greenman had followed Bentham and Hooker's (1883), and Hoffmann's (1894) circumscription of the genus which delimited it as an epappose genus. They regarded the pappose individual as Calea multiradiata and the epappose specimen as a new variety of Sabazia liebmannii. After studying these two specimens, I have found both of them to be Sabazia multiradiata.

There is a possibility that S. liebmannii may be distantly related to S. multiradiata. The relationship has been discussed under the latter species.

8b. Sabazia liebmannii Klatt var. hintonii Longpre, var. nov.

Type. MEXICO. GUERRERO: Yesceros-Cruz Pacifica; elev 2900 m, Distr Mina, 26 Nov 1939, Hinton et al. 14898 (NY, holotype!; MICH, UC, isotypes).

Planta affinissima arte ad Sabaziae liebmannii var. liebmannii; differens in foliis subcoriaceis, acuminatis, paribus plus dentium secus marginem (usque 7), et costa prominenti albida in pagina folii inferni; phyllaria externa marginibus distinctis scariosis, breviora et angustiora; lobi corollae radii generatim non quam longi.

Perennial, up to 45 cm or more tall, erect, stems (including peduncles) sparsely strigose-pilose below to more densely appressed near the head, striate, peduncles 3.5-12 cm long; leaves opposite, lanceolate-ovate to lanceolate above, bases obtuse or cuneate, apices acuminate, margins of 2-7 pairs of shallow, mucronulate callous-tipped teeth, lamina 2-7 cm long, 0.4-2.6 cm wide, subcoriaceous, very sparsely pilose-strigose to strigose-hispid above and more densely so below (especially along the nerves), sometimes with long ciliate trichomes up to 1.5 mm long, midvein of leaf below prominent, white, petiole 1-7 mm long, densely pilose-strigose to hirsute; heads terminal or in a loose subcyme, hemispherical; involucres (2-) 3 (-4) seriate,

unequal, 7-12 mm wide, 4-6 mm high, phyllaries imbricate, outer phyllaries ovate, with acute or obtuse apices, 3.2-4.2 mm long, 2-2.2 mm wide, glabrous to appressed strigose-pilose, margins strongly scarious, usually ciliate near the base, herbaceous, carinate; inner phyllaries longer, usually wider, elliptic-ovate, oblong-lanceolate or lanceolate, 4.5-6.5 mm long, 1.5-3 mm wide, glabrous, hyaline, 8-nerved, margins entire to minutely lacerate-ciliate; pales elliptic-lanceolate near the periphery, lanceolate toward the center, usually with 1 or 2 lateral acute lobes 1/8 to 1/2 the length of the middle lobe, 4.5 mm long, scarious; receptacle pyramidal, 2-3 mm wide at the base, 2-3 mm high; ray florets 8-13, pistillate, fertile, the corolla tube 1.5-2.4 mm long, sparsely to densely pilose, ligules white above and below, oblong-obovate to oblong, 7-15 mm long, 2.8-6 mm wide, with 3 apical lobes, obtuse or acute, 0.5-2 mm long; disc florets 15-40, broadly tubular, yellow, fertile, corolla tube 1 mm long, densely pilose or hirtellous, limb 2-3 mm long, pubescent along the corolla margin, lobes 5, acute, pubescent on the outside, densely papillate inside, anthers 1-1.8 mm long, subsagittate at the base, appendages rotund-acute, style 2.5 mm long, the branches subulate, pubescent on the abaxial side and along the margin; ray and disc achenes oblong or narrowly obconical, 1.5-2 mm long, glabrous, striate, brownish, epappose, ray achenes obscurely to sharply 3-ridged, disc achenes 4-5 ridged. Plate 7.

Plate 7. Photograph of an isotype of *Sabazia liebmannii* var. *hintonii*.


Sabazia
MICHIGAN STATE UNIVERSITY HERBARIUM
THE NEW YORK BOTANICAL GARDEN
No.
11-26-39.
Sabazia

ECOLOGY AND DISTRIBUTION. In mesic or humid areas associated with oakpine woods at elevations from 2000 to 2900 meters. Flowering from November to February. In Guerrero in the Sierra Madre del Sur and in vocanic areas in the southwestern part of the state of Mexico (Fig. 6).

SPECIMENS EXAMINED. MEXICO. GUERRERO: Yesceros-Cruz Pacifica, elev 2900 m, 26 Nov 1939, Hinton 14898 (NY, holotype; MICH, UC). STATE OF MEXICO: La Sierrita, Temascaltepec, elev 2450 m, 8 Dec 1932, Hinton 2770 (GH, MO, NY, US); Cumbre-Trojes, Temascaltepec, 10 Nov 1935, Hinton 8637 (MICH, NY, UC); Cerro La Corona, Zacualpan, elev 2000-2500 m, 1 Feb 1954, Matuda 30262 (US).

Variety hintonii is named after the collector of the type specimen, George B. Hinton, who collected extensively in the Mina district of Guerrero. Through his collections from various remote areas in this district, he has been responsible indirectly for the large number of new plant species established by other workers. Based on the few collections presently available, var. hintonii appears to be very closely related to var. liebmannii. Both varieties typically have lanceolate-ovate, narrowed leaves as opposed to the other two varieties which are characterized by more broadly ovate leaves, although

var. hintonii is distinguishable from var. liebmannii by its subcoriaceous, longer lanceolate-ovate and more acuminate leaves.

8c. Sabazia liebmannii Klatt var. ovatifolia Longpre, var. nov.

Type. MEXICO. OAXACA: Along hwy 190 between Km 422 & 423, ca 47 miles NW of Oaxaca, 23 Aug 1961, Longpre 199 (MSC, holotype!).

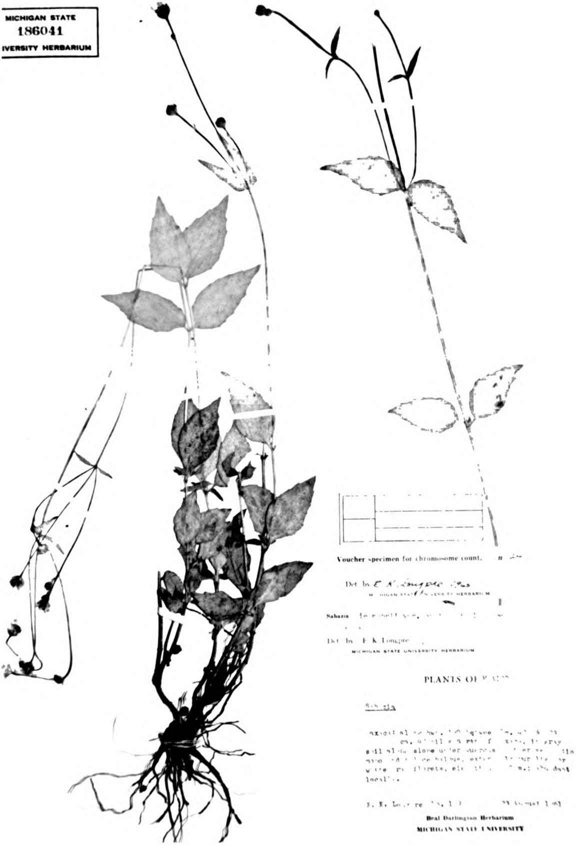
Plantae similis Sabaziae liebmannii var. liebmannii praeter folia latiora et ovatiora, longitudine laminae folii minus quam bis latitudine, basis folii obtusis vel cuneatis, folia dense strigosa usque scabridiuscula supra; caules saepe chlorini, dense strigosi usque hirsuti.

Perennial, up to 66 cm high, from a simple or branched, slender to stout woody rhizome; stems 1-several, erect, simple or branched from below, yellowish-green, grooved and striate, densely hirsute to strigose, sometimes glabrous near the base; peduncles 4.3-21 cm long, moderately to densely white-pubescent below the heads; leaves ovate or elliptic-ovate, those subtending the inflorescence 1-7 cm long, (0.3-) 0.7-4 cm wide, the base obtuse or cuneate, the apex acute or sometimes abruptly acuminate, the margin ciliate, serrate or crenate-serrate, of 3 to 8 pairs of shallow, remote, ascending, callous-tipped teeth, densely strigose to sca-

brescent above, densely strigose or strigose-pilose below, usually petiolate or sometimes sessile, petioles 1-5 (-11) mm long, sparsely or densely pilose; heads 2-16, in a loose cyme, sometimes subtended by a bract, head diameter including rays 1-1.5 cm; involucre campanulate, 5-6 mm high, 5-7 mm wide; phyllaries imbricated in 3 series, the outermost broadly ovate or oblong-ovate, acute, 3.2-5 mm long, 1.5-3.2 mm wide, herbaceous, striate, glabrous, apical margin sometimes roseate-purple, apex sometimes lacinate-ciliate, rarely with subglandular trichomes; second and third series oblong-ovate or lanceolate-ovate, 4-5 mm long, 1-2 mm wide, membranaceous; inner phyllaries hyaline, 5-10 nervate, apex sometimes lacerate-ciliate; ray florets 5-8, corolla white, 6.5-9 mm long, tube 1-2 mm long, densely pilose, the ligules broadly obovate to oblong-obovate, 4.5-8 mm long, 4.3-5 mm wide, with 3 acute or obtuse apical lobes, 0.8-1.8 mm long; style branches recurved, flattened, acute; disc florets 32-50, the tube 0.5-1.9 mm long, densely pilose, the limb narrowly funnelform to tubular, 1.8-2 mm long, 0.7-0.9 mm wide, anthers 1.2-1.5 mm long, subsagittate, appendiculate, style branches subulate; both ray and disc achenes narrowly obovate, 2 mm long, 3-4 ridged, glabrous, brown, striate; chromosome number $\underline{n}$ = 24. Plate 8.

ECOLOGY AND DISTRIBUTION. In red or gray loamy clay soil under partial shade of Quercus-Arctostaphylos woodland

Plate 8. Photograph of the holotype of *Sabazia liebmannii* var. *ovatifolia*.


MICHIGAN STATE
186041
IVERSITY HERBARIUM
Voucher specimen for chromosome count.
Det by E K Longpre
MICHIGAN STATE UNIVERSITY HERBARIUM
PLANTS OF
Beal Darlington Herbarium
MICHIGAN STATE UNIVERSITY

at elevations from 1400 to 1500 meters. Flowering from July to August. Restricted to the Sierra Madre del Sur in Oaxaca. Although var. liebmannii is found within the same general geographical area, a minimal distance of 50 miles separates the two taxa (Fig. 6).

SPECIMENS EXAMINED. MEXICO. OAXACA: Hwy at Puerto Herrera (Km 420) just NW of Vanluitlan, elev ca 2500 m, 20 Aug 1960, Iltis et al. 1132 (TEX); Along hwy 190 between Km 422 and 423, ca 47 miles NW of Oaxaca, 23 Aug 1961, Longpre 199 (MSC, holotype); Along route 190, 40 miles east of junction 125-190, 13 Aug 1961, Powell & Edmondson 673 (TEX); Cerro Verde, July 1908, Purpus 3490 (UC).

Variety ovatifolia is readily distinguished from the latter by distinctly broader, ovate leaves and more obtuse leaf bases. The blade length is generally less than twice the width. The stem is yellowish-green, densely strigose to hirsute, and the leaves are densely strigose or strigose-pilose. The margin is crenate-serrate with unequal teeth. The heads are two to many (never one)

and the rays are entirely white. Variety liebmannii on the other hand, is characterized by narrower, cuneate, lanceolate-ovate leaves, with mature leaves twice as long as wide; the stem is green to a reddish-purple, and generally glabrous to moderately strigose-pilose. Its leaves are sparsely or spreading strigose-pilose. The flowering heads are one to many, and the abaxial side of the ray is white or usually roseate-purple.

8d. Sabazia liebmannii Klatt var. michoacana (Robins.) Longpre, comb. nov.

Type. MEXICO. MICHOACAN: Mountains near Patzcuaro, 23 Nov 1891, Pringle 4099 (GH, holotype!; F, isotype).

Plants perennial, up to 88 cm tall, erect or ascending, branching from the base (rarely along the stem), with a horizontal or vertical lignescent rhizome from which extend fibrous roots; stems hirsute to pilose-strigose near the apex, with glandular capitate trichomes intermixed, striate, sometimes purple; leaves opposite, elliptic-ovate to lanceolate-ovate, coarsely serrate-dentate with 3-5 (-8) pairs of callous-tipped teeth, densely pilose-strigose to hirsute above, subcanescent to densely strigose below, 2-6.3 cm long, 0.5-3 cm wide; petioles densely hirsute-pilose (1-) 3-12 (-17) mm long, often with one or more pairs of small (4-17 mm long) sessile bracts in the axils of the

petioles; heads 1-12, terminal, solitary or in a loose cyme, hemispherical to subovoid; involucre 6-8 (-10) mm wide, 4.5-6 mm high, in 3-4 series, imbricate, unequal to subequal, outer phyllaries shorter than the inner, lanceolate-ovate to ovate, 2.5-6 mm long, 1.5-2 mm wide, strigose-pilose, ciliate, frequently with purplish margins and veins, 10-nerved, inner phyllaries oblong-ovate, 5-6.5 mm long, 1.4-2.5 mm wide, glabrous, membranaceous, entire to ciliate-laciniate toward the apex; pales persistent, oblong-lanceolate, entire (never lobed), 3-4.3 mm long, scarious, acute, 1-4-nerved; rays pistillate, fertile, 5-8, white above and below, tube 2.3-3 mm long, densely pilose, limb oblong-obovate or broadly elliptical, 8-8.5 mm long, 3.8 mm wide, with apical acute or obtuse lobes, 0.5-2 mm long, style branches obliquely ascending to slightly recurved, flattened, acute; disc florets yellow, perfect, funnelform, tube 1 mm long, pilose, style branches flattened, subulate, style base bulbous, anthers 1.2-1.8 mm long, rounded or subsagittate; achenes oblong-obconical, 4-5 ridged, black, striate, minutely strigose, epappose.

ECOLOGY AND DISTRIBUTION. On cool mountain slopes and grassy meadows surrounded by Abies. Flowering from September to November. Restricted to the western part of the trans-volcanic belt in the state of Michoacan. Its range is isolated from that var. liebmannii and var. ovatifolia by the Rio

Balsas lowland which separates the transvolcanic belt from the Sierra Madre del Sur (Fig. 6).

SPECIMENS EXAMINED. MEXICO. MICHOACAN: Southwest side of Cerro San Andres, 6 Sept 1960, Beaman 4243 (MSC); mountains near Patzcuaro, 23 November 1891, Pringle 4099 (GH, holotype; F); mountains near Patzcuaro, 12 Oct 1892, Pringle 4264 (F, GH, MO 2 sheets, MSC, NY, UC 2 sheets).

It is interesting to note that F. N. Williams (1902) regarded Abasoloa taboarda Llav. & Lex. to be synonymous with Sabazia michoacana Robins. This supposition was based entirely on the description by Lexarza (La Llave & Lexarza 1824). The type of Abasoloa taboarda is unknown. Although Williams attributes many of the non-sabazioid characters to Lexarza's inaccuracy due to poor collecting and drying, there are too many pertinent characters not in agreement with var. michoacana. The leaves are described by Lexarza as linear-lanceolate; the narrowed, ray ligules were in two

to three rows, and the disc corollas were four-lobed. In view of these distinct and contrasting characters, I concur with Robinson and Greenman (1904) who regarded the synonymy as invalid, and who felt that the description might better fit the genus Eclipta.

B. L. Robinson (1892), in establishing Sabazia michoacana as a species, distinguished it from S. liebmannii on the basis of the published description of Klatt without examining the latter specimen. One of his distinguishing characters was the loose, corymbose inflorescence of S. michoacana as opposed to the solitary flowers of S. liebmannii. Unfortunately, this contrast was based on only one specimen (Liebmann 694). Recent collections of S. liebmannii var. liebmannii exhibit the loose "corymbose" inflorescence (actually, both varieties have a loose cymose inflorescence). Furthermore, Robinson and Greenman (1904) erred in defining the latter variety, because all four of the collections available were without a root system, and were supposedly decumbent plants. Later collections, which have included a root system, have revealed the presence of a lignescent rootstock. In addition, var. liebmannii (Longpre 293) was clearly shown to be an ascending to erect plant when collected in the field and grown under greenhouse conditions. Consequently, despite other minor quantitative and qualitative differences, S. michoacana does not warrant recognition at the specific level. All varieties within the

S. liebmannii complex commonly share the erect habit, lignescent rootstock with fibrous roots, petiolate or subsessile leaves, and solitary heads or subcymose inflorescences.

9. Sabazia humilis (H.B.K.) Cass.

Sabazia humilis (H.B.K.) Cass. Dict. Sci. Nat. 46: 480. 1827. Eclipta humilis H.B.K. Nov. Gen & Sp. 4: 264. Pl. 394. 1820. Baziasa humilis (H.B.K.) Steudel, Nom. ed. 2. 1: 192. 1840. Type. MEXICO. MICHOACAN: "Crescit in aridis Regni Nova Hispaniae, prope Ario et Pazcuaro, alt. 1000 hex. Floret Sept.", Humboldt & Bonpland (P, holotype; MSC, photo 2806!).

Sabazia anomala Greenm. Proc. Amer. Acad. 41: 262. 1905. Type. MEXICO. HIDALGO: rocky mesas near Buena Vista Station, 2530 m, 7 Aug 1904, C. G. Pringle 8853 (GH, holotype!; F, MO, MSC, UC, US, isotypes).

Sabazia leiachenia Blake, Contr. U.S. Nat. Herb. 22: 614. 1924. Type. MEXICO. STATE OF MEXICO: on Nevada (Nevado) de Toluca, 15 Oct 1903, J. N. Rose & J. H. Painter 7918 (US, holotype!).

Plants annual, (2.1-) 12-45 cm high with a tap root system with extensive secondary fibrous roots; stems 1-several, erect, ascending or subdecumbent, branching from the base, usually purplish tinged, with spreading purplish glandular-capitate trichomes intermixed with white strigose-

pilose trichomes becoming more dense toward the apex; leaves opposite, sessile or subpetiolate and long attenuate at the base, the lower elliptic-ovate and sometimes oblanceolate, the upper lanceolate-ovate to linear-lanceolate, (0.7-) 1-4.3 (-6.5) cm long, 0.2-2.1 (-2.6) cm wide, acute or obtuse, lobed with 1 to 5 pairs of callous-tipped salient teeth, 3-nerved from the base, glabrous to sparsely pilose and strigose along the costa or trichomes distributed over both surfaces; peduncles terminal or axillary, densely strigose and interspersed with glandular-capitate trichomes, (0.5-) 2-8 cm long; heads hemispherical, 1-30, (0.5-) 1-1.5 (-1.8) cm in diameter (including the rays); involucre hemispherical, 2-3 seriate; phyllaries imbricated, equal to subequal, the outer sometimes purplish-tinged along margin and apex, ovate or lanceolate-ovate, 3.5-4.8 (-5.8) mm long, (0.7-) 1.2-3.1 mm wide, usually minutely glandular with white capitate trichomes, obtuse to acute, margin submembranous, ciliate; inner phyllaries somewhat longer, ovate-lanceolate, membranous, 2-5.8 mm long, 0.8-2.5 mm wide, glabrous; receptacle conical at maturity (flat when young), paleaceous, 2.2-4 mm long, 2.2-4 mm wide; pales persistent, scarious, divided 1/4 to 1/2 the length, with 2-3 linear-acuminate lobes, 2-3 mm long, 0.3-0.8 mm wide, the middle lobe about twice the length and 2-3 times as wide as the laterals; ray florets 5-13 (usually 8), pistillate, fertile, (3.0-) 3.8-6.5 (-7.5) mm long, ligules white above, white or roseate-purple below, (2.5-)

3-5.3 (-6.5) mm long, 2-4.3 mm wide, quadrate to oblong, the apex with (2-) 3 obtuse or acute teeth 0.3-1.5 mm long, the tube densely pilose (0.5-) 1-1.5 mm long (usually 1 mm); disc florets (35-) 45-95, corollas yellow, campanulate, tube densely pilose, (0.5-) 1-1.5 mm long, throat glabrous, the 5 acute lobes slightly reflexed, papillose inside, 0.3-0.5 (-1) mm long; style glabrous, branches recurved, papillate along most of the adaxial surface; anthers (0.6-) 0.8-1 mm long, bases rounded; ray and disc achenes black, striate, obovate, terete or obscurely 3-5-ridged, (0.5-) 1-1.8 mm long, 0.3-0.5 mm wide, glabrous, puberulent or hispidulous, epappose or pappose, pappus, when present, of (5-) 10 equal, persistent scales, 0.5-1 mm long, obovate, spinulose-fimbriate at the apex, whitish (brownish with age); chromosome number $\underline{n} = 4$.

ECOLOGY AND DISTRIBUTION. Locally abundant in open meadows generally associated with pine forests at elevations from 1900 to 2830 meters. Flowering from August to February. Most populations are concentrated in the state of Mexico and the Federal District in the transvolcanic belt. Outlying populations occur in the neighboring states of Hidalgo, Tlaxcala, Puebla, Veracruz and Morelos (Fig. 5).

SPECIMENS EXAMINED. MEXICO. FEDERAL DISTRICT: La Cima Station between Mexico City and Cuernavaca, elev 3035 m, 25 Sept 1961, Beaman 4539 (MSC); 1 mile north of Morelos

line on old Cuernavaca hwy, elev 9500 ft, 23 Sept 1959, Johnston 4050A (TEX); near La Cima, along old Cuernavaca hwy (Rt. 95) between Km 43 and 44, 1 Sept 1961, Longpre 407 (MSC); old hwy 190 to La Cima between Km 36 & 37, 1 Sept 1961, Longpre 419 (MSC); Toro, elev 2800 m, 23 Sept 1951, Matuda 21945 (NY); Parres, 30 Aug 1910, Orcutt 4336 (F, MO); Valley of Mexico, elev 7800 ft, 20 Oct 1896, Pringle 7408 (MO); La Venta, elev 2500-3000 m, 19 Sept 1943, Schiefer 126 (GH): HIDALGO: along road to Singuilucan 1.9 miles south from hwy 130 junction, 2 Sept 1961, Longpre 437 (MSC); rocky mesas near Buena Vista Station, 2530 m, 7 Aug 1904, Pringle 8853 (F, GH, MO, MSC, UC, US). STATE OF MEXICO: Nevado de Toluca, 10 Sept 1957, Beaman 1725 (MSC); Valley of Toluca, Berlandier 1215 (GH); Valley of Mexico, San Nicolas, 27 Sept 1865, Bourgeau 958 (F, GH, US); Meson Viejo, District of Temascaltepec, 10 Sept 1932, Hinton 1895 (GH, MO, NY, US); Nevado de Toluca, 18 Aug 1960, Longpre 143 (MSC); along hwy 190 from Puebla to Mexico City between Km 65 and 66, elev 2740 m, 31 Aug 1960, Longpre 350a (MSC); Nevado de Toluca, N side of mtn at NE side of Loma Alta, 31 July 1962, Longpre 490 (MSC); ca Amecameca, 16 Dec 1951, Matuda 25727 (NY); Oro de Hidalgo, elev 1900 m, 28 Sept 1952, Matuda 26404 (US); Sultepec, elev 2400 m, 2 Nov 1952, Matuda 27700 (NY); 20 miles south of Mexico City, 1 Sept 1946, Ortenburger, Paxon & Barkley 16M658 (F); 20 miles south of Mexico City, 1 Sept 1946, Ortenburger, Paxon & Barkley 16M809 (F, TEX);

Nevado de Toluca, elev 11,000 ft, 6 Sept 1892, Pringle 4245 (F, GH, MO, MSC, NY, UC, US); Salto de Agua, Dec 1905, Purpus 1570 (F, GH, MO, NY, UC); On Nevado de Toluca, 15 Oct 1903, Rose & Painter 7918 (US); Nevado de Toluca, 16 Oct 1903, Rose & Painter 7965 (US). MICHOACAN: "Crescit in aridis Regni Novae Hispaniae, prope Ario et Pazcuaro", alt. 1000 hex. Floret Sept, Humboldt & Bonpland (MSC, phototype). MORELOS: Lake Zempoala, elev 3000 m, 7 Oct 1951, Matuda 25611 (NY). PUEBLA: Near Rio Otlati, 14 Aug 1942, Weaver 968 (US). TLAXCALA: Sualcingo, 8 Nov 1953, Matuda 29583 (NY, US). VERACRUZ: Los Molinos, Cofre de Perote, elev 7500 ft, 16 Sept 1938, Balls 5456 (UC, US).

Pappose and epappose forms occur in separate populations and within the same population in separate plants. In 232 plants examined from 8 areas, 51% were without a pappus in both ray and disc florets; 38% possessed a pappus in both ray and disc florets, and 8% had a pappus in the

disc florets only. Comparable variation in the presence or absence of the pappus is also found in the related genera Galinsoga and in Tridax trilobata (Cav.) Hemsl. (Powell, 1965). Achenial pubescence also has the same inter- and intrapopulation variation, but to a lesser extent.

Extreme variation in height and corresponding foliage size was found in several collections, but certain populations seem to be consistently tall and larger leaved, or short and small leaved. The shorter plants (2-11 cm) tend to have glabrous ray and disc achenes while the very tall plants (30-45 cm) usually possess hispidulous to hispid achenes. No correlation with respect to the glabrous or pubescent achenes was established for specimens intermediate in height between the above ranges. From field observations, it appears that short plants are associated with open, grazed meadows and the taller individuals occur in ungrazed fields where S. humilis is the same height as the associated vegetation.

Plants grown in the greenhouse from seed exhibited a different habit from those collected in the field. Although the ascending or subdecumbent habit was noted, the plants were never erect and never attained a height of more than 21 cm. In the cultured material, leaf size is consistently small, generally not exceeding 2.5 cm in length. In addition, the plants have a more profuse branching habit. The flowering heads are more numerous (about twice the number),

and are smaller than those observed in the field. In the past, characters such as the presence or absence of a pappus, achenial pubescence, plant height, and leaf size were used to distinguish Sabazia anomala and S. leiachenia from S. humilis. Herbarium, field, and experimental studies, however, have shown these characters to be variable in populations, or else under an environmental rather than a genetic control. In view of the above observations, it appears that these so-called diagnostic characters are weak or invalid taxonomic criteria.

10. Sabazia microspermoides Longpre, sp. nov.

Type. MEXICO. GUERRERO: On mossy boulders in pine forest, Teotepec, distr. Mina, elev 3200 m, 5 Nov 1939, G. B. Hinton et al. 14788 (US, holotype!; NY, UC, isotypes).

Herba annua, radicabus fibrosi; caules pauci usque numerosi, exorientes basi, usque 9.5 cm longi, 0.75 mm lati; folia opposita, elliptica-ovata usque lanceolata, bases cuneatae usque attenuatae, apices mucronati vel obtusi, margines paribus 1-2 dentium minutorum, laminae 2.2-9 (-13) mm longae, 1.5-5 (-7) mm latae, petioli 1-5 mm longi; capitula solitaria terminalia campanulata, 6-12 mm longa (includentia flores radii), receptaculum pyramidale, paleae panduratae peripheria et anguste ellipticae-lanceolatae verus centrum,

carinatae, 2.6-2.7 mm longae; involucrum campanulatum, 1-2 seriatum; phyllaria ovata, herbacea, marginibus integris; flosculi radii 4-6 (plerumque 5), 4.1-5.8 mm longi, ligulis obdeltoideae usque oblongae, lobis tribus penitus fissis (super 1/3-1/2 longitudinem ligulae); flosculi disci circa 17, 1.2-1.3 mm longi; achenia flosculi radii et disci sine pappo, obconica, anthracina, 1.7-1.9 mm longa, omnino hispida.

Annual, decumbent to ascending, with few to many stems arising from the base, fibrous rooted; stems very slender and delicate, up to 9.5 cm long, 0.75 mm wide, moderately appressed pilose below to more densely so near the heads; leaves opposite, elliptic-ovate to lanceolate, bases cuneate to attenuate, apices mucronulate or obtuse, margins with 1-2 pairs of minute callous-tipped teeth, glabrous to sparsely pilose above and below, lamina 2.2-9 (-13) mm long, 1.5-5 (-7) mm wide, petioles 1-5 mm long, sparsely pilose; heads simple, terminal, 2-several per plant, campanulate, 6-12 mm wide (including rays); receptacle pyramidal, 1 mm long, 1 mm wide at the base; pales persistent, spatulate at the periphery to narrowly elliptic-lanceolate toward the center, carinate, 2.6-2.7 mm long, 0.3-1.2 mm wide; involucre 1-2 seriate, 2.5-6 mm high; outer phyllaries ovate, herbaceous, 2.8-4.2 mm long, 0.8-1.8 mm wide, apices obtuse, glabrous on the lower half to pilose on the upper half, margins entire, sometimes purple near the apices or throughout; inner

phyllaries like the outer but longer and wider, with scarious margins; ray florets pistillate, fertile, 4-6 (usually 5), white above, roseate-purple below, corolla tube 0.5 mm long, densely pilose, ligule obdeltoid to oblong, 3.8-5.3 mm long, 3-4.5 mm wide, with 3 deeply cleft lobes over 1/3 to 1/2 the ligule length, apices obtuse, styles 1 mm long, branches slightly recurved, acute; disc florets ca 17, corolla tube 0.2-0.3 mm long, minutely pubescent, throat campanulate, limb 1 mm long, styles 1.5 mm long, branches acute or subulate, anthers 0.8 mm long, with sagittate bases, appendages rotund-ovate; ray achenes epappose, obconical, obscurely 3-angled, black, 1.7-1.9 mm long, hispidulous over the entire achenial surface; disc achenes similar to ray achenes. Plate 9.

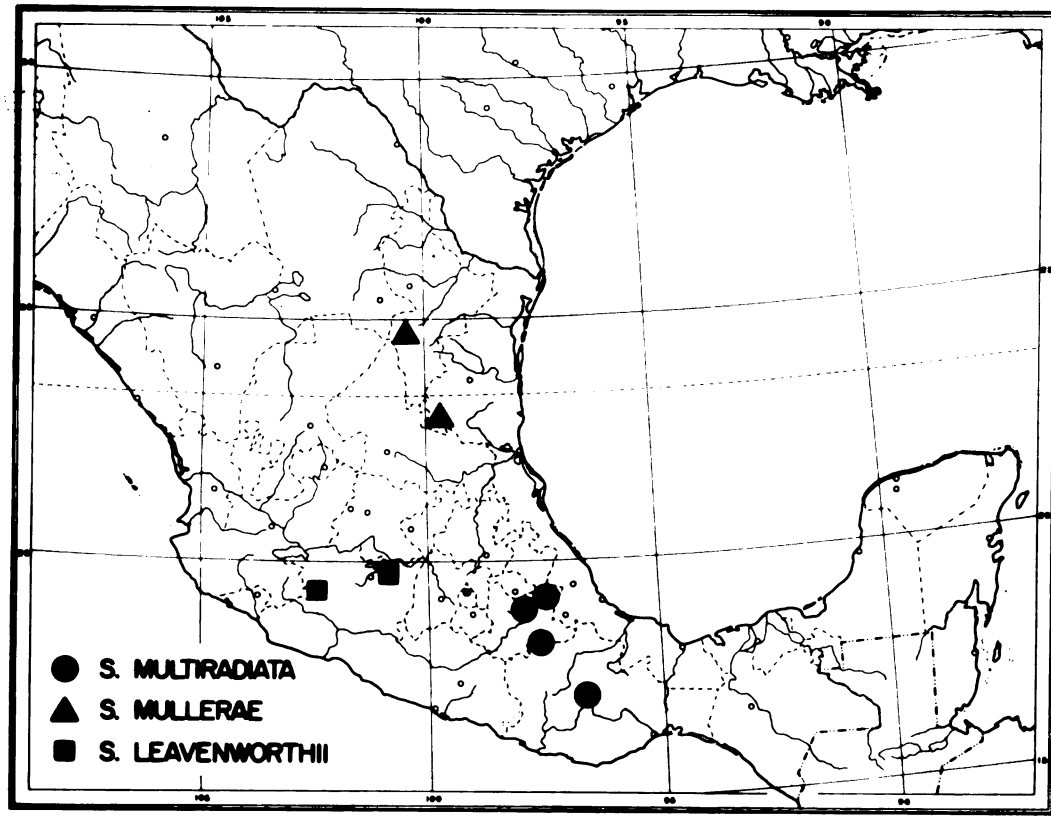
ECOLOGY AND DISTRIBUTION. See data cited for the type collection. Figure 5.

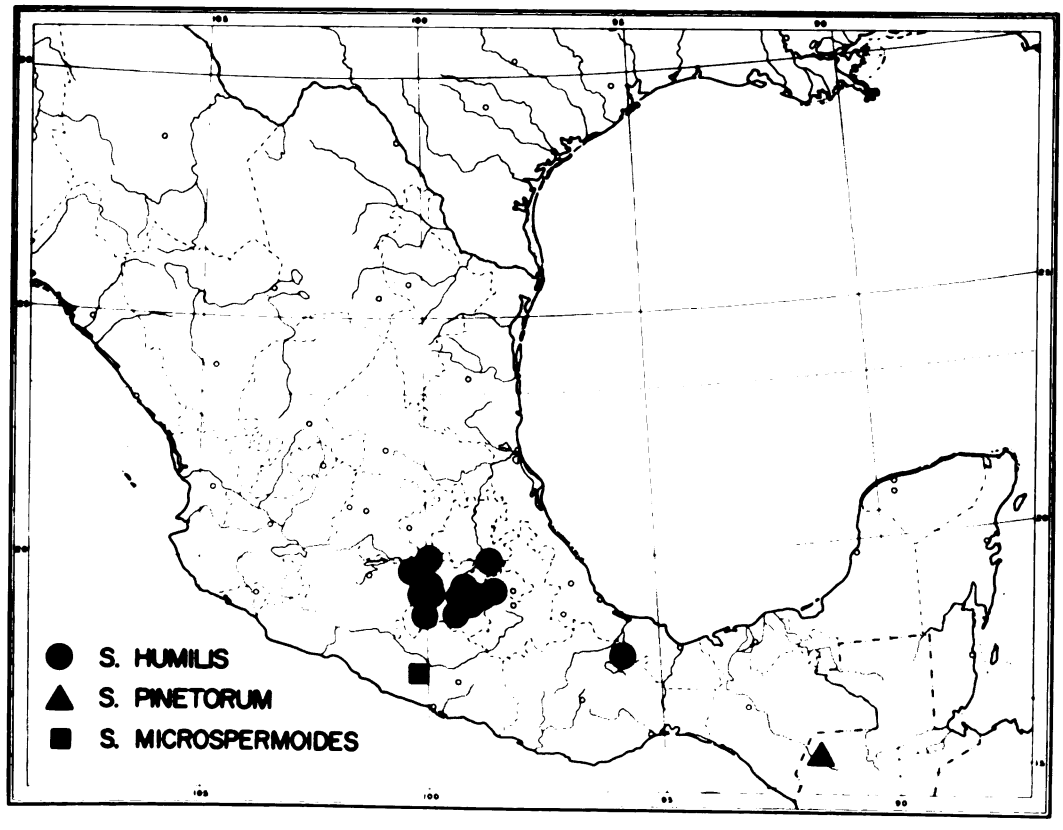
SPECIMENS EXAMINED. Known only from the type collection.

The epithet microspermoides is given because the habit of this species superficially resembles that of the genus Microspermum (tribe Helenieae). The genus Microspermum, however, is readily distinguished from Sabazia in lacking pales, possessing a one-seriate involucre, the outer disc florets being zygomorphic (with three large, outer lobes and two, small inner lobes), and when pappose, having only

Plate 9. Photograph of the holotype of *Sabazia microspermoides*.

Figure 4. Geographic distribution of S. multiradiata, S. mullerae, S. leavenworthii, S. humilis, S. pinetorum, and S. microspermoides.


S. MULTIRADIATA
S. MULLERAE
S. LEAVENWORTHII


S. HUMILIS
S. PINETORUM
S. MICROSPERMOIDES

three fragile awns. Sabazia microspermoides shows no obvious close relationship to any other species. It approaches S. humilis in being a prostrate to ascending annual with roseate-purple rays below, and in possessing elliptic-ovate leaves, but otherwise there is no satisfactory basis for assuming a closer relationship of S. microspermoides to this species than to other species in the genus.

SPECIES EXCLUDED FROM SABAZIA

Sabazia microglossa DC. Prodr. 5. 497. 1836. = Galinsoga parviflora Cav. Ic. 3: 41. 1794.

Sabazia obtusata Blake, Brittonia 2: 346. 1937. = Selloa obtusata (Blake) Longpre.

Sabazia purpusii Brandg. Zoe 5: 162. 1903. = Tricarpha purpusii (Brandg.) Longpre.

Sabazia urticaefolia DC. Prodr. 5. 497. 1836. = Galinsoga urticaefolia (H.B.K.) Benth. Bot. Voy. Sulph. 119. 1845.

TAXONOMY OF *SELLOA*

Selloa H.B.K. Nov. Gen. et Sp. 4: 266. 1820, *nom. Conserv.*, *non Selloa* Spreng.

Plants perennial, erect or ascending, repent or stoloniferous, from a short vertical rootstock with slender or stout fibrous roots; stems simple or branching from the base, often subscapose; basal leaves broadly obovate to oblong-obovate, attenuate-petiolate at the base, apices acute or obtuse, margins usually entire or with 1 or more pairs of remote denticulate teeth, glabrous, cauline leaves much like the basal except for being more linear-oblong, linear-lanceolate or bracteolate; heads terminal, axillary or subcymose, hemispherical or broadly turbinate; involucre 2-3-seriate, outer phyllaries ovate to broadly elliptic-ovate, obtuse, dark roseate-purple to blackish-purple along margins and sometimes at the apices or bases, inner phyllaries lanceolate-ovate to oblong-ovate, generally broader than the outer, acute or minutely apiculate; receptacle convex, pales persistent, linear-setiform, acuminate; ray florets 7-19, fertile, white above, white or lavender below, ligules cuneate-oblong, with 3 acute or obtuse apical lobes; disc florets ca 30 to 75, yellow or greenish-yellow, perfect, fertile, salverform to broadly funnelform; ray achenes turbinate or laterally compressed, with 3 pronounced ridges or about 5

obscure ridges, glabrous, epappose or with 5-10 setiform caducous awns with minute lacerate margins; disc achenes similar except for being somewhat more obconical or obovoid; basic chromosome number $x = 8$; type species, Selloa plantaginea H.B.K.

KEY TO THE SPECIES OF SELLOA

1A. Plants up to 52 cm tall, erect; stems, peduncles and outer phyllaries without dark-purple glandular trichomes; basal leaves 1.5-6.5 cm long, glabrous, lustrous; involucre 7-10 mm high, 10-16 mm wide, outer phyllaries 6-11 mm long; pales 4.5-5 mm long; ray florets 7-13, ligules roseate-lavender beneath, 9.7-17.0 mm long, sterile stamens present; disc florets 40-75, golden yellow, anthers 1.5-1.8 mm long; achenes with 5-10 setiform caducous awns . . . . . S. plantaginea

1B. Plants up to 22 cm tall, repent or stoloniferous or ascending; stems, peduncles and outer phyllaries with dark-purple glandular trichomes; basal leaves 0.7-3.6 cm long, sparsely to evenly pilose on both surfaces, non-lustrous; involucre 4-6 mm high, 8-11 mm wide, outer phyllaries 4-5.6 mm long; pales 1.3-3 mm long; ray florets 11-19, ligules white below, 5 mm long, stamens absent; disc florets 30-35, greenish-yellow, anthers 0.9-1.2 mm long; achenes epappose. . S. obtusata

1. Selloa plantaginea H.B.K.

Selloa plantaginea H.B.K. Nov. Gen. et Sp. 4: 266. pl. 395. 1820. Feaea plantaginea (H.B.K.) Spreng. Syst. Veg. 3: 581. 1826. Feea plantaginea (H.B.K.) Kuntze, Gen. Pl. 1: 388. 1891. Feaella plantaginea (H.B.K.) Blake, Contrib. U.S. Nat. Herb. 26: 231. 1930. Type. MEXICO. MICHOACAN: "Crescit inter Aguasarco et Ario, in declivitate occidentali montium Mexicanorum, alt. 1000 hex. Floret Septembri" Humboldt & Bonpland (P, holotype; MSC photo 2807!).

Sabazia subnuda Robins. & Seat. Proc. Amer. Acad. 28: 108. 1893. Type. MEXICO. STATE OF MEXICO: In pine forest, Nevado de Toluca, elev 12,000 ft, 2 Sept 1892, Pringle 4226 (GH, holotype!; MSC, NY, US 2 sheets).

Plants perennial, erect, up to 52 cm tall, from a short vertical rootstock with numerous stout secondary roots, tertiary roots arising only from near the terminal ends of secondary roots; stems simple, scapose or sometimes branching from the base, sparsely pilose below, becoming more densely appressed pubescent near the heads, green, sometimes reddish-purple; basal rosette of 4-10 leaves, 5 to 18 cm in diameter; leaves broadly oblanceolate, acute, attenuate at the base, margins entire or of 1-2 pairs of remote shallow teeth, (0.5-) 1.5-6.5 cm long, (0.3-) 1-2.5 cm wide, glabrous, upper surface lustrous, petioles widened at the base, the

lower ones sheathing, cauline leaves bracteolate, opposite or alternate, oblong to linear-lanceolate, truncate, obtuse, entire (0.7-) 1.3-2.5 (-5) cm long, 0.1-0.6 cm wide, glabrous, triplinerved with prominent midrib on abaxial side; heads solitary, terminal or up to 6 in a subcyme, hemispherical or broadly turbinate; involucre in 2-3 series, 10-16 mm wide, 7-10 mm high; outer phyllaries ovate or broadly elliptic-ovate, 6-11 mm long, 4.5-8 mm wide, glabrous to sparsely pilose, entire or sparsely ciliate toward the base, light green, dark-purple along the margins and sometimes at the base; inner phyllaries ovate, lanceolate-ovate to oblong-ovate, apices acute to acuminate, 5.8-9.2 (-13) mm long, (1.2-) 2-4 mm wide, glabrous, entire, hyaline, sometimes purplish at the apices; receptacle convex to conical, 2.5-5 mm long, 2-3 mm wide at the base, pales narrowly linear, 4.5-5 mm long, 0.1-0.2 mm wide, acuminate; ray florets 7-13, corolla tubes 2.5-3.5 mm long, very sparsely to moderately pilose, ligules cuneate-oblong, white above, roseate-purple below, (4.5-) 7.2-13.5 mm long, 3-5 mm wide, apices trilobed, acute or obtuse, 1-2 (-3.5) mm long, with 5 sterile stamens; disc florets 40-75, narrowly funnelform, corolla tubes 1-1.8 mm long, sparsely to moderately pilose, throat and lobes 2-3 mm long, anthers 1.5-1.8 mm long, with rotund-ovate appendages, bases rounded, style branches acute to subulate; ray achenes broadly obovate, with 3 ridges, laterally compressed, glabrous, 1.8-2 mm long, black, pappus caducous,

of 5-10 setiform awns with minute lacerate margins; disc achenes similar except for being more obconical and 5-angled; chromosome number n = 16.

ECOLOGY AND DISTRIBUTION. Among tufted grasses along steep, open montane slopes, in open pine forests, in volcanic ash and in rocky soil along road banks at elevations between 3280 and 4000 meters. Flowering from July to November. In the transvolcanic belt in the states of Michoacan, Mexico, Puebla, Veracruz and the Federal District (Fig.6).

SPECIMENS EXAMINED. MEXICO. FEDERAL DISTRICT: San Miguel, Sept 1931, Lyonnet 1537 (US); Canada de Contrera, Sept 1933, Lyonnet 817 (US). STATE OF MEXICO: Ojos de Agua, Nevado de Toluca, elev 12,000 ft, 7 Sept 1938, Balls 4965 (US); Nevado de Toluca, northwest side of mtn between Loma Alta and Cerro Gordo, 7 Sept 1957, Beaman 1677 (MSC); Tlaloc, south side of mtn in pass between Tlaloc and Telapon, elev ca 3600 m, 22 Aug 1958, Beaman 2347 (MSC); Iztaccihuatl, NW side of mtn ca 0.3 km east of Trancas, elev ca 3550 m, 16 July 1959, Beaman 2859 (MSC); At Puerto del Aire on the Mexico-Puebla hwy 54.5 km east of Mexico City, 24 July 1959, Beaman 2904 (MSC); west slope of Nevado de Toluca, 4 Oct 1940, Cutler 3993 (US); Volcan de Toluca, elev 12000 ft, Heller 357 (GH); Crucero Agua Blanca, Temascaltepec distr, elev 3380 m, 30 Aug 1933, Hinton 4613 (GH, NY 2 sheets, US); Mezón Viejo, Temascaltepec distr, 11 Oct 1935, Hinton 8344

(GH, US); Nevado de Toluca, along road between Km 9 & 10, 1.4 mi beyond turnoff to crater, elev 3420 m, 18 Aug 1961, Longpre 149 (MSC); Nevado de Toluca, NW side of mtn between Loma Alta & Cerro Gordo, elev 3820 m, 18 Aug 1961, Longpre 150 (MSC); along hwy 190 just before Km 53 (from San Martin to Los Reyes), elev 3030 m, 31 Aug 1961, Longpre 352 (MSC); Nevado de Toluca, NW side of mtn between Loma Alta & Cerro Gordo between km 9 & 10, 31 July 1962, Longpre 500 (MSC); Nevado de Toluca, on north side, 18 Oct 1953, Matuda 29482 (US); Nevado de Toluca, 4 Oct 1940, Moore 94 (GH); Nevado de Toluca, elev 12,000 ft, 2 Sept 1892, Pringle 4226 (GH, MSC, NY, US 2 sheets); Nevado de Toluca, Oct 1903, Rose & Painter 7959 (NY, US). STATE OF MEXICO?: Apitzo, Mt. Ixtaccihuatl, 27 July 1938, Balls 5127 (US). MICHOACAN: At southwest side of Cerro San Andres, ca 12 kms north of Ciudad Hidalgo, 5 Sept 1960, Beaman 4239 (MSC). PUEBLA: Iztaccihuatl, east side of mtn above San Augustin, west of Texmelucan, 12 Sept 1958, Beaman 2542 (MSC). VERACRUZ: Cofre de Perote, elev 12,000 ft, 9 Nov 1938, Balls 5433 (US).

Although Selloa plantaginea is distinct from Selloa obtusata in having fewer to no cauline leaves, a caducous setiform pappus and

sterile stamens in the ray florets, the remaining characters are constant for the genus. The early nomenclature of S. plantaginea has been adequately covered by Blake (1930).

2. Selloa obtusata (Blake) Longpre, comb nov.

Sabazia obtusata Blake, Brittonia 2: 346. 1937. Type. GUATEMALA. HUEHUETENANGO: Chancol, Sierra Cuchumatanes, elev 10,600 ft, 15 Sept 1934, Skutch 1265 (GH, holotype!; F, US, isotypes).

Perennial, ascending, repent or stoloniferous, from a short vertical rootstock with slender fibrous roots, up to 22 cm tall, simple or with 2-3 branches arising near the base; stems (including peduncles) pilose with dark-purple glandular-capitate trichomes, striate, greenish-yellow; basal leaves broadly obovate to oblong-obovate, 7-36 mm long, 2-9.5 mm wide, attenuate at the base, apices obtuse, entire except for a pair of callous-tipped teeth, ciliate (usually with white or pinkish glandular trichomes intermixed with very sparse, appressed short trichomes); cauline leaves much like the basal except for being more linear-spatulate or linear-oblong, 5-38 mm long, 3-11 mm wide, more bracteolate near the heads; heads terminal or axillary, 1 to 3 per plant, hemispherical; involucre 2-3 seriate, equal, 8-11 mm wide, 4-6 mm high; first series of phyllaries ovate, obtuse, 4-5.6 mm long, 1.8-2.5 mm wide, sparsely pilose with glandular-

capitate trichomes intermixed, blackish-purple at apices and margins, third series of phyllaries longer, broader than the first and second, 5.5 mm long, 3 mm wide; receptacle convex, pales linear, acuminate, 1.3-3 mm long, 0.2 mm wide, entire, scarious; ray florets 11-19, white above and below, corolla tubes 1.2-2 mm long, sparsely to moderately pilose, ligules cuneate-oblong to linear-oblong, 3.8-4.8 mm long, 1-2.4 mm wide, with 3 acute or obtuse apical lobes, 0.2-1.2 mm long, style 1.2-2 mm long, branches recurved, flattened near the apex, acute; disc florets 30-35, greenish-yellow, salverform or broadly funnelform, corolla tube 0.5-1 mm long, pilose,1-1.5 mm long, with 5 acute lobes 0.7-0.8 mm long, glabrous outside, style branches broadly flattened, apex acute to somewhat subulate, anthers 0.9-1.2 mm long, bases rounded to subsagittate, appendages rotund-acute; ray achenes plump or turbinate, with 5 obscure rounded edges, 1.8-2 mm long, black, glabrous, epappose; disc achenes similar, 1.2-1.5 mm long, chromosome number $\underline{n} = 8$.

ECOLOGY AND DISTRIBUTION. In subalpine meadows and open pine forests at elevations from 3300 to 3800 meters. Collected in flower from July through December. Known only from the Sierra de los Cuchumatanes in Huehuetenango, Guatemala (Fig. 6).

SPECIMENS EXAMINED. GUATEMALA. HUEHUETENANGO: Sierra de los Cuchumatanes between Kms 324 and 325 (between Chemal

& San Juan Ixcoy) on Ruta Nacional 9N, 4 Aug 1959, Beaman 3026 (MSC); Sierra de los Cuchumatanes, between Tojiah & Chemal at Km 318, 30 July 1960, Beaman 3800 (MSC); Sierra de los Cuchumatanes, 31 July 1960, Beaman 3845 (MSC); Sierra de los Cuchumatanes, along Ruta Nacional 9N between Km 322 & 323, 26 Aug 1961, Longpre 228 (MSC); Chancol, Sierra Cuchumatanes, elev 10,600 ft, 15 Sept 1934, Skutch 1265 (GH, holotype; F, US); region of Chemal, Sierra de los Cuchumatanes, 28 Dec 1940, Standley 81079 (F); Near Tunima, Sierra de los Cuchumatanes, elev 3300-3500 m, 6 July 1942, Steyermark 48311 (F, US); vicinity of Chemal, summit of Sierra de los Cuchumatanes, elev 3700-3750 m, 8 Aug 1942, Steyermark 50251.

Selloa obtusata is separated from the only other species of the genus by a distance of about 600 miles. Both species of Selloa are similar to Sabazia in being restricted to montane habitats which are characterized by cool, open meadows or open pine forest. Morphologically Selloa plantaginea with its larger heads and floral parts, in addition to its vestigial ray stamens, appears to be more primitive than S. obtusata.

TAXONOMY OF TRICARPHA

Tricarpha Longpre, gen. nov.

Plantae annuae vel perennes, herbae foliis secus caules, palaribus vel radicibus fibrosis, erectae, prostratae vel serpentes usque ascendentes; folia opposita, ovata, elliptica ovata usque lanceolata-ovata, integra usque serrata paribus 5-8 dentium, sparsim usque moderate pilosa utrinque, sessilia vel petiolulata; capitula solitaria usque cymosa; receptaculum convexum usque subconicum, paleis persistentibus scariosis, profunde trilobis, lobis longitudine 2/3-3/4 palearum partes aequantia; phyllaria imbricata, seriebus 2-4, lanceolata-ovata usque oblonga-elliptica, marginibus scariosis; radii flosculi pistillati, fertiles, uniseriati, circa 6-13, ligulis cuneatis-oblongis usque linearibus-oblongis, aequaliter roseolis vel albis, inconspicuuse trilobis; disci flosculi perfecti, circa 45, flavi, antheris includentibus appendicibus 1-1.8 mm longis, appendicibus rotundis-acutis usque oblongis-acutis, stylis ramis divergentibus usque recurvatis, acutis; radii et disci achenia epappo, obovata, glabra, striata, fusca vel anthracina.

Annual or perennial caulescent herbs with taproots or fibrous roots; ascending to erect or prostrate-trailing; leaves opposite, ovate, elliptic-ovate to lanceolate-ovate,

entire to serrate with 5-8 pairs of minute callous-tipped teeth, sparsely to moderately pilose on both surfaces, sessile or petiolate; heads terminating the branches, axillary or in a cyme; receptable convex to subconical, chaff persistent, pales scarious, deeply trifid, lobes 2/3-3/4 the length of the pale; phyllaries imbricate, in 2-4 series, lanceolate-ovate to oblong-elliptic, scarious margined; ray florets pistillate, fertile, uniseriate, ca 6-13, ray ligules cuneate-oblong to linear-oblong, uniformly roseate or white, inconspicuously 3-lobed; disc florets perfect, ca 45 or less, yellow, anthers including appendages 1-1.8 mm long, appendages rotund-acute to oblong-acute, style branches diverging to recurving, acute; ray and disc achenes epappose, obovate, glabrous, striate, brown or black; type species, Tricarpha purpusii (Brandg.) Longpre.

Key to the Species of Tricarpha

1a. Perennial (from a fibrous root system?); lower leaf margins non-ciliate, petioles 3-6 mm long; inflorescence of 1 or 2 heads; phyllaries with 3-5 dark green longitudinal streaks, margins and interstreaks scarious; ligules white, 5.5-7 mm long; disc florets funnelform, 2.4 mm long. . . . . 1. T. durangensis

1b. Annual from a short taproot; lower leaf margins ciliate, sessile or with petioles 1-2 mm long; inflorescence

commonly cymose or paniculate-cymose, rarely of a single head; phyllaries broadly scarious along the margins, longitudinal green streaks absent; ligules lavender or roseate, 10 mm long; disc florets tubular, 3-3.4 mm long. . . . . 2. T. purpusii

1. Tricarpha durangensis Longpre, sp. nov.

Type. MEXICO. DURANGO: Mexico hwy 40, 75 miles E Revolcaderos, common in moist ravines, rays white, elev ca 7200 ft, 7 Nov 1964, Flyr 292 (MSC, holotype!).

Planta perennis, caulibus simplicibus vel ramificantibus, prostrata vel ascendens?, pilis pubescentibus effusis vel adpressis; rami capitulis terminalibus; folia ovata-elliptica laminis 2.5-4.7 cm longis, 1.2-2.4 cm latis, integra vel paribus 6 dentium minutorum callusorum; petiolis 3-6 mm longi, moderate pilosi; pedunculi 1.5-6.5 cm longi moderate pilosi; pari bractearum subtentis capitulis; involucrum campanulatum, 4 mm altum, 7 mm latum; phyllaria 2-3 seriata, lanceolata-ovata, vittis 3-5 scariosis, 3-3.8 mm longis, 1.2-1.8 mm latis, marginibus ciliatis vel lacerato-ciliatis; receptaculum paleis, pyramidale; paleae externae ellipticae-lanceolatae, acuminatae, 2.7-2.8 mm longae, lobis 2 lateralibus 0.5-0.9 mm longis; paleae interiores profunde trilobatae, lobis lateralibus longitudine 3/4 lobi medii partes aequantia; flores radii 12-13, 1-seriati, ligulis oblongis, 5.5-7 mm

longis, 2.8 mm latis, albis; disci flores infundibuliformes, corollis 2.4 longis, flavis; achenia radii et disci obovata, 1.0-1.1 mm longa, glabera, fusca (?), striata, sine pappo.

Perennial (prostrate-trailing or ascending?), stems simple or branching, yellowish-green, striate, moderately pilose, internodes about 8 cm long; leaves opposite, ovate or elliptic-ovate, blades 2.5-4.7 cm long, 1.2-2.4 cm wide, bases obtuse to cuneate, apices acute or acuminate, margins entire to subentire with 6 pairs of minute callous-tipped teeth, sparsely to moderately pilose above and below especially along the costa, petioles 3-6 mm long, moderately pilose; peduncles 1.5-6.5 cm long with 1 pair of bracteolate leaves subtending the heads, 2-8 mm long; receptacle convex, outer pales elliptic-lanceolate, acuminate, 2.6-2.8 mm long, the 2 lateral lobes 0.5-0.9 mm long, inner pales longer, with lateral lobe sinuses 3/4 the length of the pale; involucres hemispherical, 7 mm wide, 4 mm high, 2-3-seriate, subequal, subtended by 1 or 2 linear-lanceolate bracts, 2.5 mm long, 0.5 mm wide; outer phyllaries lanceolate-ovate, acute, 3 mm long, 1.4-1.8 mm wide, glabrous to very sparsely pilose, with 3-5 dark green longitudinal streaks, margins and interstreaks scarious, sparsely ciliate; inner phyllaries lanceolate-ovate, 3.8 mm long, 1.2 mm wide, glabrous, membranaceous, margins scarious, finely lacerate-ciliated, with 3 green streaks alternated with scarious ones; ray florets 13, white,

the tube 2 mm long, densely pilose, the ligule cuneate-oblong, 5.5-7 mm long, 2.8 mm wide, lobes very shallow, 0.1-0.5 mm long; style branches slightly recurved at anthesis, acute, style 1.9 mm long; disc florets yellow, funnelform, the tube 1 mm long, moderately hirtellous, throat and lobes 1.4 mm long, the 5 lobes acute, 0.3 mm long; filaments adnate at tube apex, anther including appendages 1 mm long, bases rounded, appendages rotund-acute; style 2 mm long, branches diverging to recurved; ray and disc achenes obovate, 1.0-1.1 mm long, glabrous, brown (?, immature), striate. Plate 10.

ECOLOGY AND DISTRIBUTION. See data cited for the type collection. Figure 6.

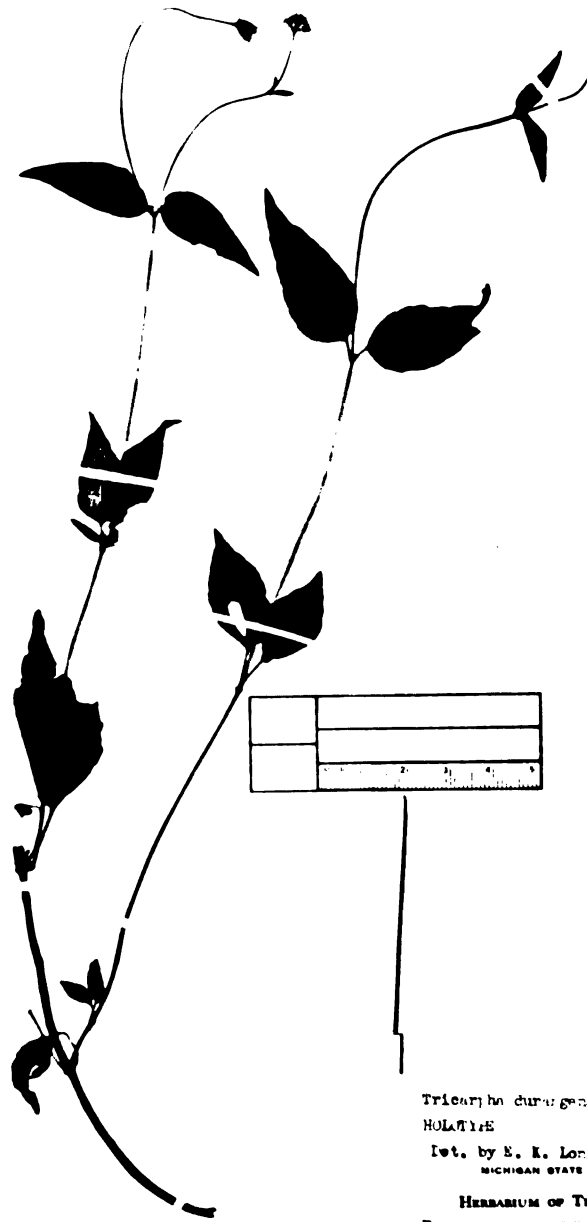
SPECIMENS EXAMINED: Known only from the type collection.

2. Tricarpha purpusii (Brandg.) Longpre, comb. nov.

Sabazia purpusii Brandg. Zoe 5: 162. 1903. Type. MEXICO. BAJA CALIFORNIA SUR: Near San Felipe, Cape Region, Feb 1901, Purpus 3961 (UC, holotype!; F, GH, NY, US 2 sheets, isotypes).

Annual, to 41 cm high, from a short taproot; stems simple or sometimes branched near the base, erect, striate, greenish to reddish-purple, sparsely pilose to densely villous toward the apex; leaves opposite, membranaceous, ovate

Plate 10. Photograph of the holotype of Tricarpha durangensis.



Tricarpha durangensis Long
HOLOTYPE
Det. by E. K. Longhorn 1965
MICHIGAN STATE UNIVERSITY HERBARIUM

HERBARIUM OF THE UNIVERSITY OF TEXAS
PLANTS OF

or lanceolate-ovate, blades 1.0-3.5 cm long, 0.2-1.8 cm wide, blades obtuse, apices acuminate, coarsely serrate, with 5-8 pairs of callous-tipped teeth, lower margins ciliate, very sparsely to remotely short-pilose on both surfaces especially along the lower costa, sessile or with petioles 1-2 mm long, sparsely to moderately pilose, lower cauline leaves often shriveling; peduncles (2-3) arising from 1 node bearing 1 or 2 small bracts, often secondarily and tertiarily dichotomous above; heads 1 to 24 per plant, usually cymose or paniculate-cymose; receptacle abruptly conical, 2 mm long, 1 mm wide, chaff persistent,pales obtriangular in outline, scarious, 2-2.4 mm long, with 3 equal acuminate lobes, sinuses 2/3-3/4 the length of the pale; involucre 3-4-seriate, hemispherical to narrowly subovoid or turbinate, 4.5-6 mm wide, 4-5 mm high; first series of 2-3 bracteolate phyllaries 2-4.5 mm long, 1-1.5 mm wide, lanceolate-ovate, acute, sparsely short-pilose, margins broadly scarious, ciliate; inner phyllaries subequal to equal, ovate-elliptic to oblong-elliptic, subapiculate, 4.5-5 mm long, 1.7-1.8 mm wide, glabrous, membranaceous, margins ciliate, broadly scarious; ray florets 6-12, pistillate, roseate to lavender on both surfaces, corolla tube 4 mm long, moderately pilose, ligule linear-oblong, 10 mm long, 2.8 mm wide, with 3 shallow obtuse lobes at the apex, 0.5-1 mm long, style branches diverging, apices acute; disc florets about 45, perfect, tubular, tube 1 mm long, moderately to densely hirtellous-hirsutulous, throat

and lobes 2-2.4 mm long, lobes acute, 0.4 mm long, pubescent or papillate abaxially, style 3.8-4.5 mm long, branches recurved, with acute apices, pubescent-papillate underneath, papillate above; anthers 1.5-1.8 mm long including appendages, appendages acute, bases rounded to subsagittate; ray and disc achenes epappose, narrowly obconical to plump, obscurely 5-angled, 1-1.2 mm long, glabrous, black, striate. Plate 11.

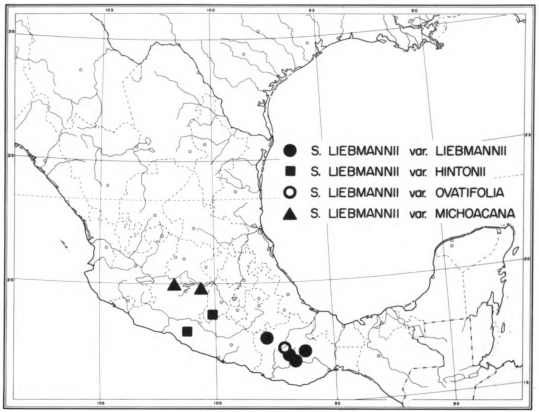
SPECIMENS EXAMINED: Known only from the type locality.

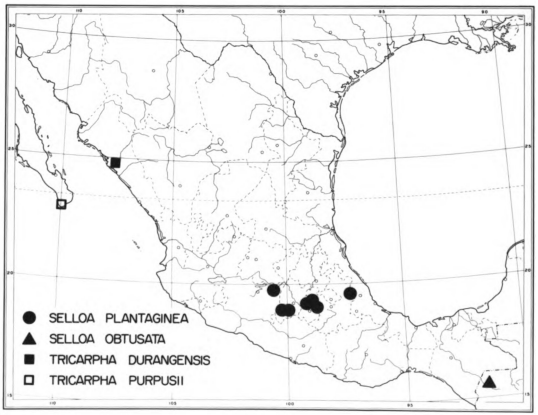
ECOLOGY AND DISTRIBUTION. There are no habitat data for this species. It has not been recollected since the original collection by C. A. Purpus in 1903. The San Felipe of the Cape region is not to be confused with the San Felipe situated on the northeast coast of Baja California and located 120 miles south-southeast of Mexicali. The former area according to a map of the Del Cabo region of Baja California (Galvez, 1922), is placed about the 23°4' N latitude and 109°50' W longitude. The San Felipe of the Cape region is located at the southern end of the Sierra de la Victoria where the elevation reaches a maximum of 1900 meters toward the Pacific side (Fig. 6). According to Tamayo (1962) this area of the Cape region is characterized by coniferous forests. It has a temperate climate in which the dry winter is not rigorous and the temperature during the coldest months ranges between -3° and 18° C. The rains are periodical commencing in the fall but decreasing in the winter.

Plate 11. Photograph of the holotype of Tricarpha purpusii.

89641
Tricarpha purpusii (Brandg.) Longpre
HOLOTYPE
Det. by E. K. Longpre 1965
MICHIGAN STATE UNIVERSITY HERBARIUM
TYPE OF
FLORA
LOWER CALIFORNIA
Tricarphus Purpusi Brandeg.
San Felipe (Cape Region)
O. A. Purpus - Feb. 1901

Figure 6. Geographical distribution of S. liebmannii var. liebmannii, S. liebmannii var. hintonii, S. liebmannii var. ovatifolia, S. liebmannii var. michoacana, Selloa plantaginea, S. obtusata, Tricarpha durangensis, and T. purpusi.


S. LIEBMANNII var. LIEBMANNII
S. LIEBMANNII var. HINTONII
S. LIEBMANNII var. OVATIFOLIA
S. LIEBMANNII var. MICHOACANA


SELLOA PLANTAGINEA
SELLOA OBTUSATA
TRICARPHA DURANGENSIS
TRICARPHA PURPUSII

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