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A revision of *Schoenocaulon* (Liliaceae:Melanthieae)

Frame, Dawn Maria, Ph.D.

City University of New York, 1990

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A

A REVISION OF SCHOENOCAULON (LILIACEAE: MELANTHIEAE)

by

DAWN MARIA FRAME

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

1990

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirements for the degree of Doctor of Philosophy.

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Abstract

A revision of Schoenocaulon (Liliaceae: Melanthieae)

by Dawn Maria Frame

Advisor: Dr. Arthur Cronquist

Schoenocaulon, an archaic genus of lilies which grow primarily in Mexico, is revised herein. In this treatment, which differs substantially from the monograph by Brinker (1942), 24 species and three varieties are recognized. Morphological and field studies have provided the foundation for the taxonomic treatment. Supplemental information concerning the biology of the genus is documented in the chapters on chemistry, morphology, cytology, and ethnobotany. The chapter on evolution discusses factors bearing on evolution within Schoenocaulon, and the major evolutionary trends as they relate both to the genus and to the family.

Acknowledgements

This dissertation has passed from an idea into a reality with the aid of many generous colleagues and friends. Indeed, so many people have been instrumental in its conception and realization, that I will not be able to name them all. To those not here named, my apology is that there is not enough space to mention everyone, but I shall know and remember my debt. I would like first to acknowledge the untiring help of my advisor, Dr. Arthur Cronquist, who has stood by me and carefully watched and tended my intellectual development. So too, has my dear friend, Rupert Barneby. Other people who are, or were, associated with the New York Botanical Garden should be mentioned: Dr. Ghillian Prance, Drs Pat and Noel Holmgren, Dr. Mike Nee, Dr. Fred Seaman, Dr. P. Mick Richardson, Dr. Chong-wook Park, Dr. Andrew Henderson, Dr. John Pipoly, Dr. Richardo Callejas, Dr. Jim Grimes, Mrs. Lothian Lynas, Mrs. Jane Brennan, Linda Marshner, Lucy Kluska, Steve Crisafulli, Chih-Hua Tsou, Chung-Fu Shen, Miriam Colella, Thomas Starbuck, and Wee Nanakorn.

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Dedication:

To my parents and grandparents

DISCLAIMER

Nomenclatural innovations presented herein are intended for future publication in proper form. Their inclusion here is not intended to constitute formal publication under the International Code of Botanical Nomenclature.

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Chapter I: Introduction

This is a study of Schoenocaulon A. Gray, a distinctive genus in the equally distinctive tribe Melanthieae of Liliaceae. The outstanding taxonomic problem in Schoenocaulon has been that of specific boundaries. The most recent study was that of Brinker (1942), which has not proved useful as more material has accumulated. A multidisciplinary approach is used in the present study, and the following aspects are examined in greater or lesser detail: floral anatomy, chemistry, cytology, morphology, and pollen. Historically Schoenocaulon is best known as Sabadilla and as a source of the drug Veratrine. In the taxonomic portion of the paper, I recognize 24 species and three varieties. All but four species are endemic to Mexico.

Chapter II: Taxonomic History

Europeans' knowledge of Schoenocaulon developed along two lines: enquiry about the source of the drug "veratrine", and study of a new liliaceous genus from the Americas. The traditional European source of veratrine was rhizomes of Veratrum. At least as early as the 18th century, a new drug with properties similar to veratrine became available from Mexico (Lemery 1716). The source of this drug was sabadilla seeds (see chapter on Ethnobotany). A century later, sabadilla seeds were used in making veratrine (Lindley 1838).

At the turn of the 19th century, Michaux collected some unusual liliaceous plants in Florida and Georgia, the like of which he had never seen before. Uncertain of the taxonomic position occupied by these lilies, he described them as Helonias dubia in his *Flora Boreali-Americana* (1803). Later botanists, such as Willdenow (1803), Pursh (1814), and Nuttall (1818), shared Michaux's doubt that these plants represented a species of Helonias, but made no taxonomic changes.

Subsequently, Asa Gray (1837) proposed a new genus Schoenocaulon to accomodate these unique plants. At about this time, Schiede and Deppe collected some plants from the southern Sierra Madre Oriental of Mexico which they identified as the source of sabadilla seeds (Lindley 1838). The plants were sent to Europe, where Schlechtendal and Chamisso (1831) described them as a new species of Veratrum, V. officinale. It is likely that Schlechtendal and Chamisso treated these plants as veratrums because they were a source of a drug similar to the one produced by European Veratrum species, as well as on the

basis of some morphological similarity. Soon after, Hartweg made collections from a nearby region and sent a sample plant to Lindley in London. Lindley recognized this specimen as conspecific with those found by Schiede and Deppe and realized that it was neither a Veratrum nor a Helonias. Moreover, for some reason, he also considered it different from Schoenocaulon "in its whole habit" (Lindley 1839). Lindley erected a new genus, Asagraea (Lindley 1839), based upon Hartweg's specimen. When Asa Gray saw Lindley's description and illustration of Asagraea, he suspected that it belonged to his genus Schoenocaulon. After subsequent examination of Schiede and Deppe's specimens, his suspicions were confirmed and he reduced Asagraea to synonymy.

Another common synonym for Schoenocaulon is Sabadilla. The word sabadilla is a corruption of the Spanish Cebadilla meaning "little barley". Brandt and Ratzeburg (1837) published Sabadilla as a subgenus of Veratrum, apparently because they did not believe that V. officinale constituted a true Veratrum but seemingly lacked the courage to propose a new genus.

Chapter III: Morphology

Seed germination

Schoenocaulon exhibits epigeal germination and is cryptocotylar.

Figure 1 shows a drawing of a young S. calcicola seedling with its first leaf emerging through the slit at the cotyledonary node (A), and a similar seedling a few days later in which the cotyledon has elongated further and about midway along its length bends sharply downwards (B). In this way, the seed coat, containing the remains of the endosperm and the haustorial tip of the cotyledon, comes to lie atop the soil.

Habit

Schoenocaulon, like all members of tribe Melanthieae, is a geophyte. Variation in habit in the tribe ranges from rhizome to bulb geophytes. Schoenocaulon is unusual in that it is a bulb-rhizome geophyte.

Underground structure

Neither the bulb nor the rhizome is particularly well-developed; that is, the bulb does not store very much starch as compared to other bulbous liliaceous plants, nor is the rhizome very large. The slow growing bulb-rhizome may be shallowly or deeply buried. Schoenocaulon produces two types of roots, contractile roots and "feeder" roots. A contractile root is usually the first or second root to develop after the root pole has elongated. As in many monocotyledonous plants, the primary root is short-lived and all subsequent roots are shoot-borne. The contractile root is somewhat lateral in position and pulls the young seedling downwards further into the soil. The rhizome often

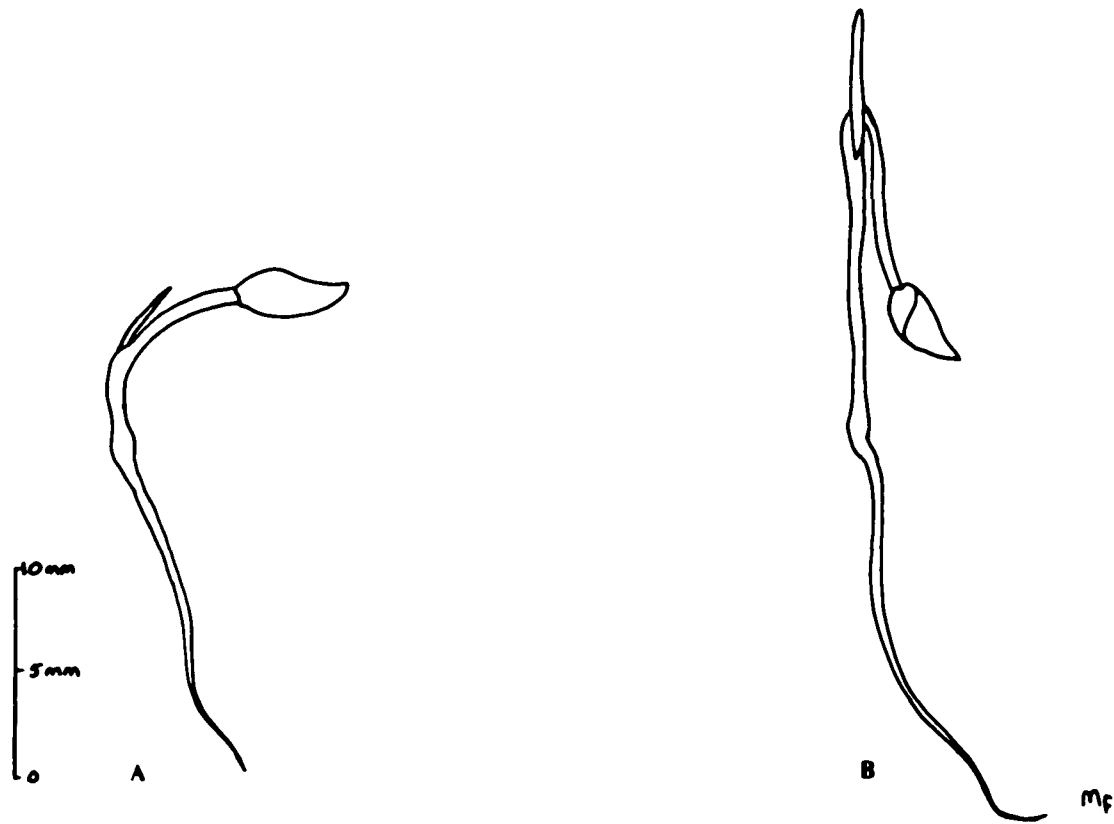


Figure 1. Germinating seedling of Schoenocaulon calcicola. A, showing first leaf emerging; B, after the cotyledon has elongated further.

grows out plagiotropically, but as a result of the asymmetric downward pull of the contractile root or roots, the rhizome often ends up oriented not quite vertical to the bulb. The rhizome is commonly dorsiventrally flattened, and appears to grow sympodially. It is not clear how the rhizome arises from the shoot nor how often lateral meristems are produced along its length. It appears that all leaf bases contribute to the bulb, and no dimorphism is apparent.

Foliage

The leaves of Schoenocaulon are entirely basal and arranged in a what appears to be a distichous to spirodistichous phyllotaxis. In shape they are narrowly to not quite broadly linear. The leaves are conduplicate as they emerge from the fibrous tunic, and often remain partially folded for much of their life. Both margins as well as the abaxial surface of the median vein are scabrous. A thin membrane tears when the leaves unfold, leaving the margins rather more irregularly scabrous than the abaxial surface of the median vein. The apex is sometimes acute, but more generally it is senescent, appearing tattered and brown. The nerves are scattered and form a mesh-like framework in the underground sheathing leaf base and gradually become strictly linear in the emergent leaves. Leaves usually persist from year to year. When the underground portion senesces, the tissue between the nerves deteriorates leaving mostly the nerves. It is these nerves which comprise the fibrous tunic. Oxalate raphides are abundant in the leaves, as they are in most organs of the plant body.

Inflorescence

Schoenocaulon is readily distinguished by its spike-like raceme,

an inflorescence type distinct in tribe Melanthieae. Other genera in the tribe have either racemes or panicles. Occasionally Schoenocaulon species have a second raceme growing out of what was a flower position along the inflorescence axis. Usually this aberration occurs towards the base of the raceme. The flowers are initiated in a spiral sequence along the inflorescence axis, and a papery hyaline bract subtends each flower. The pedicels are mostly very short until the fertilized ovary begins to mature into a fruit. During this period the pedicels usually double or triple their length. Although the pedicels in some species may reach 3-4 mm in length, they are almost always curved upwards, disposing the fruit parallel to the scape, something which reinforces the spike-like impression of the inflorescence.

Flowers

Flowers are actinomorphic (radially symmetric), with the sepals and petals indistinguishable (so-called tepals) and occurring in two whorls. The uppermost flowers of the raceme are usually functionally staminate, whereas the lowermost flowers are always perfect. The tepals are mostly green to green-purple and leathery, only rarely becoming petaloid in texture as in Schoenocaulon pellucidum, S. tenuifolium, and S. tigrense. Occasionally the tepals are cream-colored, as in S. officinale and S. pellucidum, and rarely red, as in S. tenuifolium. All other members of tribe Melanthieae have tepals that are petaloid in texture, however, as far as I am aware, none other than S. tenuifolium have red tepals. However, species with purple and burgundy-colored tepals are scattered throughout the tribe.

Nectaries are perigonal; a single nectary may be found on the adaxial surface near the base of each tepal. In most instances, the nectaries are barely discernible, and they may only be represented by nectariferous tissue. The species with the best-developed nectary is S. officinale. This species has an unique nectary "pad" which seems to represent the specialization of several cell layers for nectar production. The nectary in this case is usually slightly elevated as a result of tissue elaboration. This is in contrast to all other Schoenocaulon species, in which the nectary is sunken.

Similar to all genera in the Melanthieae, the anthers of Schoenocaulon are cordate to plumply sagittate, or what is loosely referred to as "reniform". The anthers are basifixed with a median furrow, extrorse, and explanate after dehiscence. They open and close as a result of hydrostatic pressure. Traditionally the anthers have been described as "confluent". The anther is composed of four thecae, but the intervening thin tissue either dissolves just prior to, or is disrupted by, dehiscence, or possibly both. Often the remains of the septa are visible on the anthers after the pollen has been shed. And although the anthers abscise soon after this, the filaments are persistent.

As is common in tribe Melanthieae, the carpels of Schoenocaulon are usually incompletely coherent and a carpellary hole is observable (figure 2). The ovary varies from wholly superior and raised with the stamens on a short column above the perianth to slightly inferior. Placentation is essentially axile, although this varies somewhat depending upon how coherent the carpels are, so that at some places

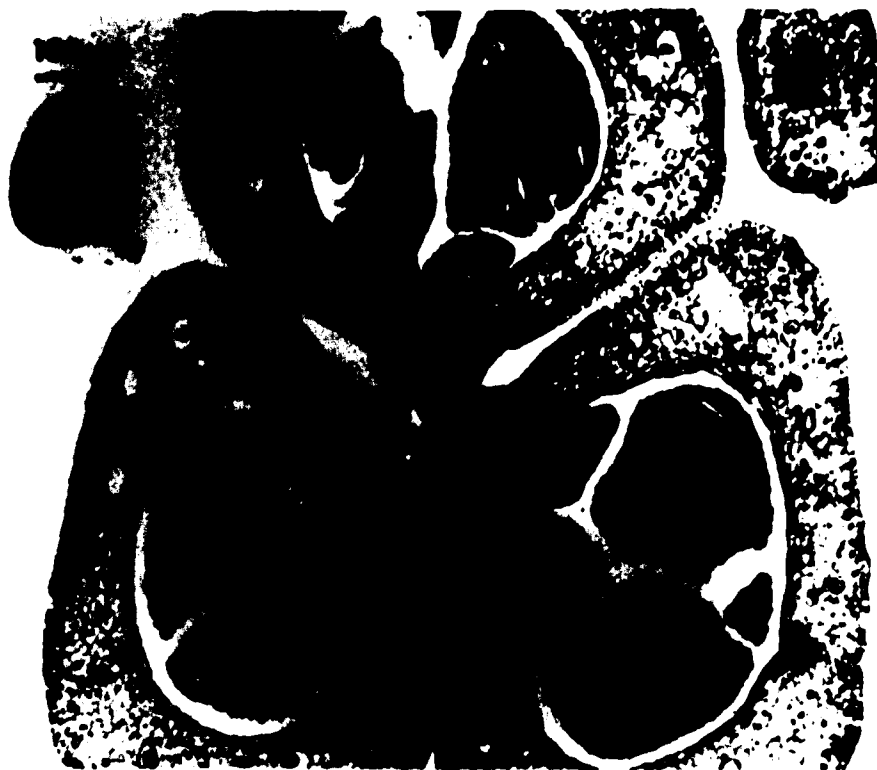


Figure 2. Cross-section through an ovary of Schoenocaulon jaliscense var. jaliscense showing carpellary hole.

Anatomical Sections: Fresh material was fixed in FAA. Flowers for study were later transferred to 50% ETOH, then taken through an increasing alcohol series. The ETOH was gradually replaced by tertiary-butyl alcohol which in turn was gradually replaced by paraffin. The material was sectioned and then mounted on a clean microscope slide. The slide was deparaffinized and the sections stained in Safranin O and counterstained with Fast Green (after Johansen, 1940), then taken through a xylene series and mounted in Canada Balsam.

along the ovary the placentation may be submarginal. The 2-16 ovules are crassinucellar and anatropous to nearly campylotropous. The styles are free, relatively undifferentiated, and have hollow stylar canals. Similarly, the stigma is undifferentiated and merely the termination of the style. It is horseshoe-shaped in cross-section.

Pollen

I examined the pollen of eight species of Schoenocaulon using the scanning electron microscope. Although this was by no means an exhaustive study, it appears that there are two pollen types in Schoenocaulon; specifically, monocolpate, and monocolpate with an operculum (figure 3 B, C). Pollen in the Liliaceae does not tend to vary much, and for this reason, I do not consider it likely that more than the two pollen types just mentioned will be found in Schoenocaulon. Both pollen types are to be found in the family, albeit the latter is rare and may be considered a comparatively advanced condition (see Roth et al., 1986). The pollen grains are on the order of 20-30 μm long. Schoenocaulon officinale has monocolpate pollen with an operculum (figure 3 B). The operculum is clearly visible in an anatomical section through an anther of this species (figure 3 A). Conversely, S. tenue has simply monocolpate pollen (figure 3 C). The sculpturing pattern in Schoenocaulon is reticulate and different species exhibit minor variations in this pattern.

Fruit

Schoenocaulon has a dry septicidal capsule. In the past, it was believed that loculicidal and septicidal capsules represented a major

Figure 3. Schoenocaulon pollen types. A, anatomical section through an anther of S. officinale, arrow indicates operculum (see figure 2. for methods); B, Scanning Electron Micrograph of a pollen grain of S. officinale; C, Scanning Electron Micrograph of a pollen grain of S. tenue.
Scanning Electron Micrographs: Fresh pollen grains were mounted with adhesive tape on metal stubbs and sputter-coated with gold to a thickness of 100 Å, then placed in a JEOL U3 and viewed at a voltage of 25 Kilovolts.



evolutionary dichotomy within Liliaceae s. l. (see Baker, 1879).

Today, however, there is little emphasis on this character (Dahlgren et al., 1985). It appears that whether a taxon has a loculicidal or septicidal capsule is merely dependent upon the degree of fusion between the adjacent carpels. Dehiscence will occur along the line of least resistance, in the case of Schoenocaulon, this is along the septa. The greater and greater fusion of the carpels in the Liliaceae has doubtless led to a shift from septicidal to loculicidal capsules. Thus, for instance, Fritillaria has loculicidal capsules.

Seed

The seeds of Schoenocaulon differ from those of Melanthium and Veratrum in that they are not winged. Nonetheless, they do have a small appendage. The shiny smooth golden to dark brown seeds of Schoenocaulon show little variation in seed coat morphology as evinced by scanning electron microscope study of six species and light microscope study of nearly all taxa. Figure 4 shows a scanning electron micrograph of the cells near the distal tip (A) and those near the middle of a seed (B) of Schoenocaulon officinale. Typically the cells towards either end of the seed are isodiametric, whereas those in the middle are long and narrow. In Schoenocaulon, the epidermal cells throughout the plant body are relatively uniform, and, with the exception of at least one population of S. officinale from Venezuela, unadorned by hairs or trichomes. As part of an anatomical survey of the seeds of medicinal plants, Fisher (1942) investigated the seeds of S. officinale. To the best of my knowledge, the genus is fairly uniform with respect to the features described by Fisher

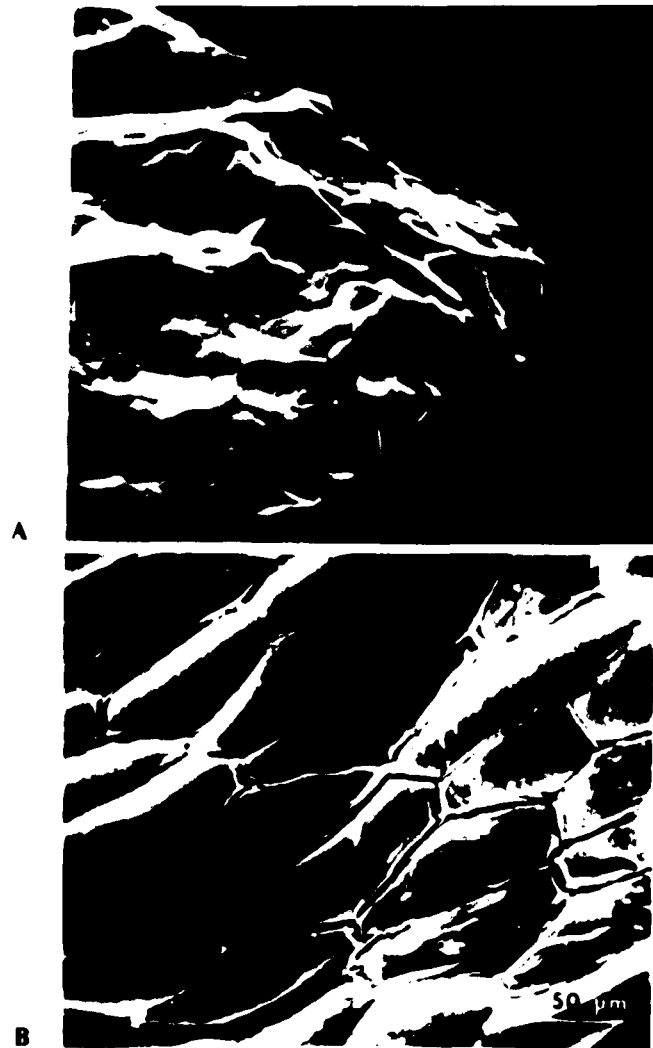
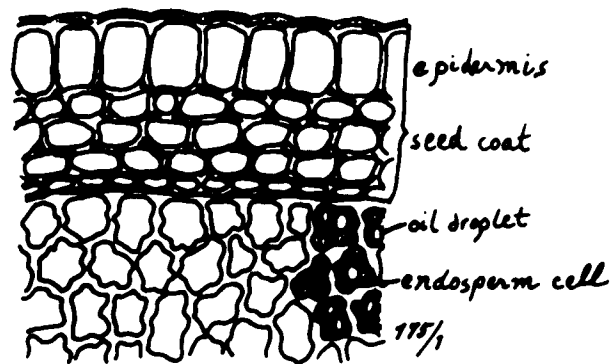
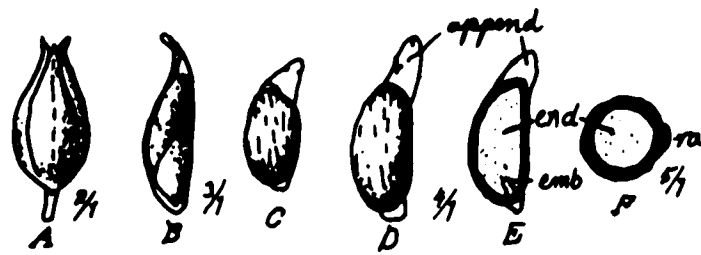


Figure 4. Scanning Electron Micrograph of the seed coat of Schoenocaulon officinale. A, cells at distal tip of seed; B, cells toward the middle of the seed (see figure 3 for methods).

(1942). A raphe is clearly visible on most seeds and the embryo is minute and embedded in a large mass of endosperm (figure 5). Within the cells of the endosperm, oil droplets are common and roundish starch grains less so (Fisher 1942; figure 5).

Figure 5. Features of the fruit and seed of Schoenocaulon officinale, adapted from Fisher (1942). A, whole fruit; B, long-section through a locule showing position of seeds; C, a seed; D, a longer seed with a longer appendage; E, long-section through a seed showing minute embryo embedded in a mass of endosperm; F, cross-section through a seed, the raphe is clearly evident; G, greatly magnified section through a seed showing the different cell layers and certain cell contents.



G

Chapter IV: Cytology

No differences were found in chromosome number among the eight species studied. A chain of three chromosomes was observed in meiotically dividing cells of Schoenocaulon tenorioi. Whether the chain is the result of a genetic interchange, or adhesions between chromosomes remains unknown. Gross morphology of chromosomes in interphase and dividing cells was compared with those of a related genus, Chionographis (Liliaceae: Helonieae).

Prior to the present study, four species of Schoenocaulon had been studied cytologically. De Zerpa (1951), studying pollen mother cells of S. officinale, found this species to have $2n=16$. As part of his dissertation A cytotaxonomic study of the genus Zigadenus (Liliaceae), Preece (1956) made chromosome counts from pollen mother cells of S. drummondii (= S. ghiesbreghtii) and S. texanum, and in both he found $2n=16$. Lastly, Cave (1967), studying pollen mother cells, reported $2n=16$ for S. dubium.

The following karyological study examines eight species of Schoenocaulon, two of which had been examined previously.

Methods

Freshly collected young inflorescences were placed in either Carnoy's (1:3:1, chloroform: absolute ethanol: glacial acetic acid, v/v/v) or Farmer's (3:1, absolute ethanol: glacial acetic acid, v/v/v) solution. After a minimum of 36 hours, the fixed material was transferred to a storage solution of 70% ethanol. The preserved material was treated, examined and photographed at the Jodrell Laboratory, Royal Botanic Gardens, Kew. For chromosome counts from

pollen mother cells, anthers were dissected from the flowers and squashes were made in 1.8% aceto-orcein. For chromosome counts from root tips, germinating seeds with actively-growing root tips were pretreated in alpha-bromonaphthalene for 24 hours at 4°C. These were then fixed in 1:3 ethanol : glacial acetic acid (v/v) at 4°C for at least 30 minutes, (the material may be stored indefinitely at 4°C in this last solution). The fixed material was then hydrolysed in 1N HCl at 60°C for 10 minutes (after this treatment the root tips usually became detached from the parent seed). The root tips were then transferred to Feulgen solution for staining and placed in the dark at room temperature for at least 30 minutes. The Feulgen stained root tips were then counter-stained with 1.8% aceto-orcein, and squashes made. Coverslips were removed in liquid CO₂ and the slides dehydrated in absolute ethanol before mounting in Euparal. Photographs were taken with a Zeiss photomicroscope.

Results and Discussion

The results of chromosome counts of Schoenocaulon from material that I collected are presented in Table I. All species studied have a chromosome number of $2n=16$. With the exception of some slight variation in chromosome morphology observable by the light microscope, there is little other obvious karyological difference among species of Schoenocaulon. Indeed, the genus is remarkable for the constancy of its chromosome number. This is in sharp contrast to all other genera in tribe Melanthieae. In her perceptive study, Chromosomes of the California Liliaceae (1970), Cave concludes of the Veratreae (=Melanthieae): "Evolution within the tribe must have taken place by

Table I. Chromosome Counts in *Schoenocaulon*•.

Species & Collection #	Pollen Mother Cell	Root Tip
<i>S. calcicola</i> , DF 275	2n = 16	2n = 16
<i>S. caricifolium</i> var. <i>caricifolium</i> , DF 288 & DF 283	2n = 16	2n = 16
<i>S. caricifolium</i> var. <i>oaxacense</i> , DF 289	2n = 16	
<i>S. comatum</i> , DF 347	2n = 16	
<i>S. ghiesbreghtii</i> , DF 265 & DF 386	2n = 16	
<i>S. intermedium</i> , DF 287	2n = 16	2n = 16
<i>S. jaliscense</i> var. <i>jaliscense</i> , DF 406	2n = 16	
<i>S. tenorioi</i> , DF 344 & DF 345	2n = 16	
<i>S. texanum</i> , DF 394		2n = 16

•from material collected by D. Frame

multiplication of the basic set of 8 chromosomes as well as by increase in the basic number through fragmentation and recombination of the original 8" (p. 45). If this hypothesis is correct, then it seems likely that Schoenocaulon has retained the original set of eight chromosomes without further multiplication. The chromosomes of Schoenocaulon are quite small, on the order of 1.5-3 μ m, and are just resolvable by the light microscope. For this reason other methods of karyotype analysis, such as Giemsa banding, were not undertaken. Nonetheless, as previously mentioned, some differences in chromosome morphology are discernible. Figure 6 shows the meiotic and mitotic chromosomes of two species of Schoenocaulon, S. calcicola (C, D) and S. intermedium (A, B).

Pollen of S. tenorioi collected at Cerro Verde in Oaxaca were frequently aborted. I did manage to find some cells undergoing meiosis, and these appeared to have a distinctive chromosomal aberration, a chain of three chromosomes (figure 7 A), the probable result of either an interchange of genetic material or adhesions between the chromosomes (see Price, 1956). A similar chain of three chromosomes is present in pollen mother cells of a population of the same species collected at nearby Rodeo (figure 7 B). Interestingly, this population is usually fertile. The consequence of a simple case of heterozygous interchange, with pairing between two pairs of homologous segments, would either be two pairs or a chain of three and a univalent (Darlington, 1937). It is difficult to discern whether a univalent is present in the material I studied because of the small size of the chromosomes. Interchange heterozygotes are semi-sterile

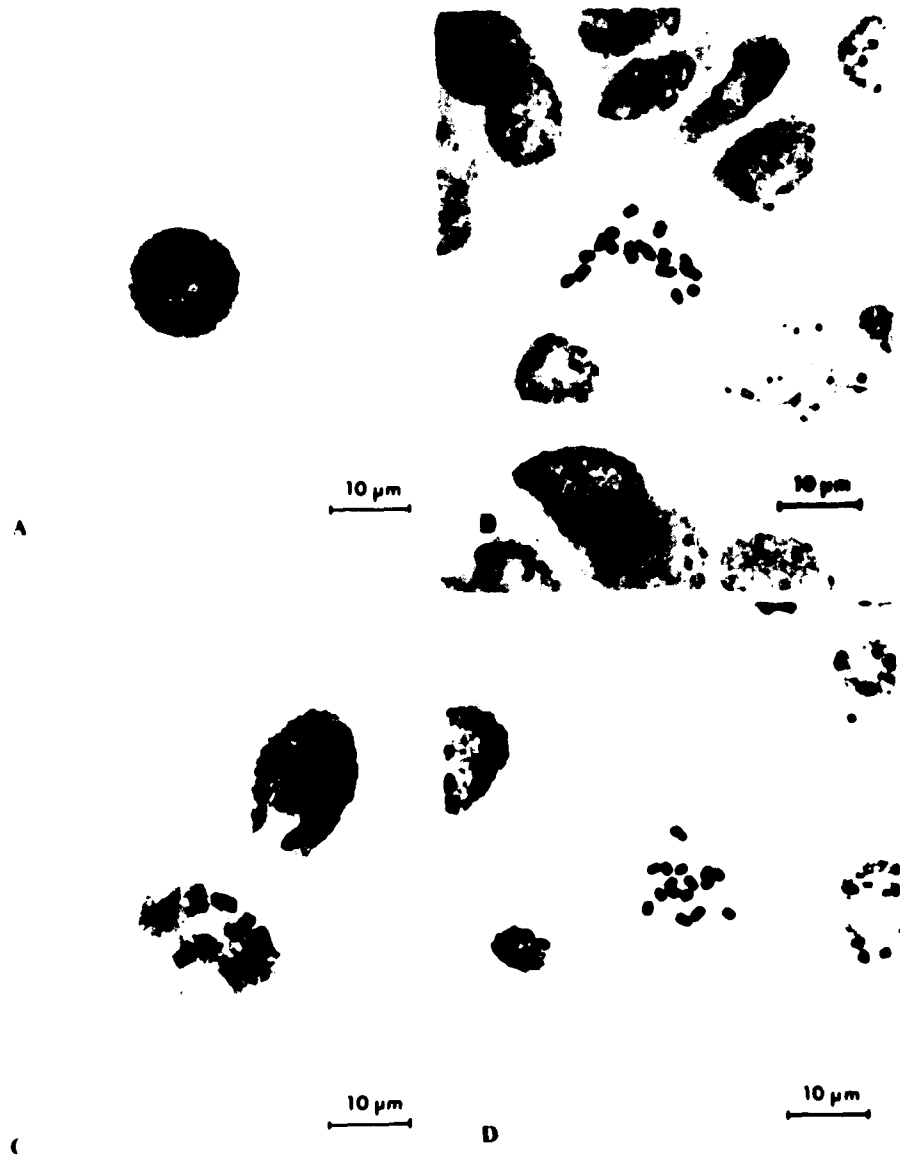


Figure 6. Chromosome squashes of *Schoenocaulon*. A, *S. intermedium* (Frame & Tenorio 288) metaphase I; B, *S. intermedium* (Frame & Tenorio 287) root tip cells; C, *S. calcicola* (Frame et al. 275) metaphase I; D, *S. calcicola* (Frame et al. 275) root tip cells.

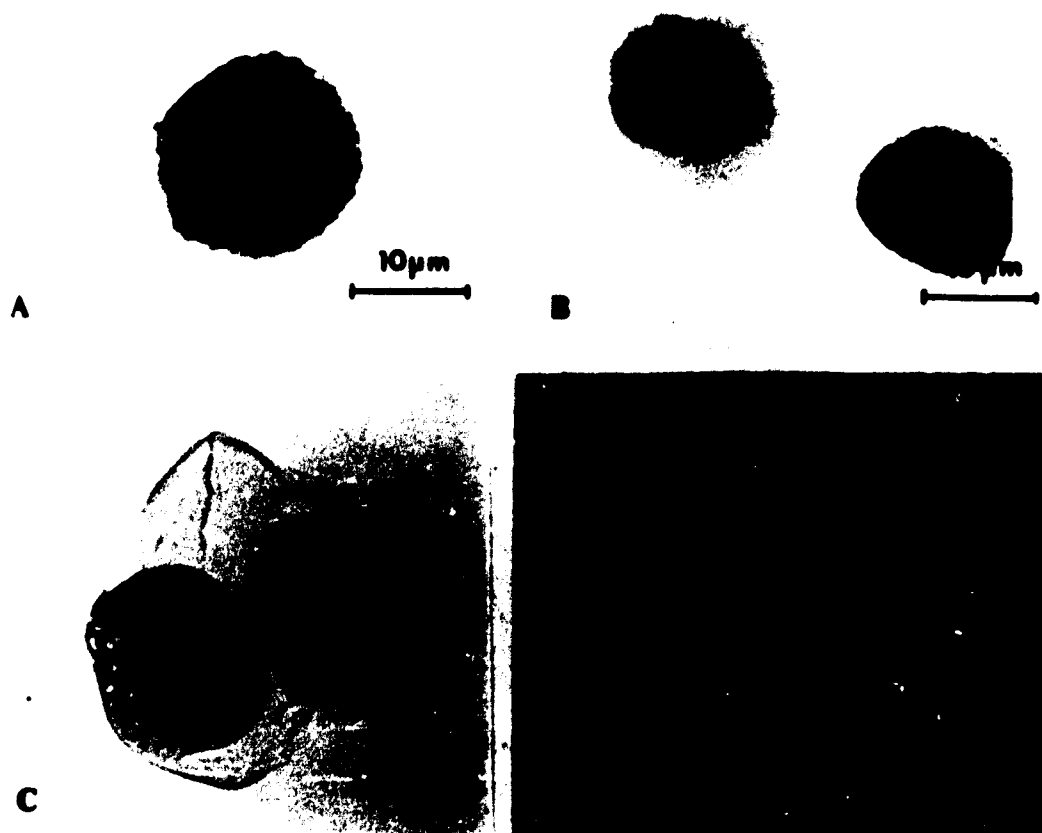


Figure 7. Chromosome squashes of *Schoenocaulon*. A, *S. tenorioi*, population at Cerro Verde (Frame et al. 345) metaphase I, chain of three chromosomes; B, *S. tenorioi*, population from near Rodeo (Frame et al. 344) metaphase I, chain of three chromosomes; C, *S. caricifolium* var. *caricifolium* (Frame & Tenorio 288) metaphase I; D, *S. caricifolium* var. *caricifolium* (Frame & Tenorio 283) root tip cells.

due to the non-viability of those gametes that lack one of the chromosome segments present in the parental complement (Darlington, 1937). Notwithstanding this interesting correlation, it is beyond the scope of the present study to determine whether the observed chain is the result of a genetic interchange or due to so-called "sticky" adhesions.

Mitotically dividing cells are usually pretreated with a spindle poison such as colchicine, or in this case, alpha-bromonaphthalene, to make them more condensed and consequently more distinct when viewed by the light microscope. Although the chromosomes of cells treated in this manner are clearly far from their native state, it is standard cytological practice to make morphological comparisons within and between sets of such chromosomes. The chromosome morphology of the pretreated root tip cells of Schoenocaulon caricifolium var. caricifolium is distinctive. When compared with the chromosomes from similarly treated root tip cells in S. calcicola and S. intermedium (figure 7 D, B), the chromosomes of S. caricifolium var. caricifolium appear smaller and seem to lack distinct kinetochores (figure 7 D). However, the chromosome squashes of somatic cells of this same species show a restriction which seems to be a kinetochore (figure 7 C). It is likely that the pretreatment causes the chromosomes of this species to become so condensed as to obscure visualization of the kinetochore. Tanaka and Tanaka (1979), studied the morphological characteristics of somatic chromosomes in four species of Chionographis (Liliaceae: Helonieae), a genus belonging to a tribe closely related to the Melanthieae. They found these species' chromosomes to be

"holokinetic", that is lacking a distinct kinetochore, and to have curious heteropycnotic segments visible in the interphase nucleus. All species of Schoenocaulon that I studied have unusual heteropycnotic segments similar to those reported in Chionographis (see interphase cells in figure 6 B), which supports the presumed close evolutionary relationship of the two genera. And although Schoenocaulon chromosomes are morphologically similar with respect to size and general appearance to those of Chionographis, they differ in that Schoenocaulon chromosomes have distinct kinetochores. Further research on this subject in both genera is needed.

On the basis of the foregoing chromosomal studies it would be premature to conclude that Schoenocaulon species have experienced little genetic divergence, as it is quite possible that slight differences in chromosome morphology are compatible with a considerable amount of genomic change. Nonetheless, it would be true to state that they show less evidence of chromosomal variability than other members of tribe Melanthieae. If the degree of chromosomal variation is indeed a rough indirect measure of the relative rates of evolution within a particular taxon, most Schoenocaulon species are evolving relatively slowly, a notion consistent with my observations of their natural history.

Chapter V: Evidence from Chemistry

The crude extracts of seeds of 12 Schoenocaulon species were analyzed by reverse-phase high performance liquid chromatography (HPLC). The standard used in the study was β -veratrine, a mixture of veratridine, cevadine and a presumptive degradation product. Although no firm conclusions may be drawn from the study, it seems that: steroidal alkaloids of a population appear to be constant from year to year; steroidal alkaloid content is very similar among individuals of a population; veratridine and cevadine appear to be present in all healthy fully mature seeds; and veratridine and cevadine may vary quantitatively within and between species. The nectar composition of two populations of Schoenocaulon tenuifolium was determined by Irene Baker (unpublished). In both cases, the major sugar was sucrose.

The notion that the alkaloid chemistry of Schoenocaulon and other members of the tribe Melanthieae might provide useful taxonomic characters was first propounded by Kupchan et al. (1961). They note some general chemical trends and hope that "further phytochemical studies of the Veratreae may yield results which may be significant for their potential contribution to the understanding of the course of plant evolution, as well as for their taxonomic utility." Genera belonging to the tribe Melanthieae are characterized by elaborating steroidal alkaloids, the most complex alkaloids produced by plants. These alkaloids are known, at least in Veratrum, to occur throughout the plant body, and in genera other than Schoenocaulon they accumulate in the bulb or rhizome. In Schoenocaulon, however, the steroidal

alkaloids accumulate in the mature seeds.

Steroidal alkaloids are of limited occurrence in the plant kingdom. They are known to occur in five flowering plant families: Asclepiadaceae, Apocynaceae, Buxaceae, Solanaceae, and Liliaceae. Each family exhibits a distinctive carbon skeletal type (Geissman & Crout 1969), and examples of the carbon skeletons found in these families are illustrated in figure 8. Liliaceous genera are characterized by the C₂₇ skeleton derived from cholesterol, but with modification of rings C and D and ring closure, giving rise to the C-nor D-homosteroids. Apart from genera of the Melanthieae, steroidal alkaloids in the Liliaceae are only known from Fritillaria (Lilioideae).

Alkaloids of the Melanthieae (often known collectively as "Veratrum alkaloids") fall into 3 distinct groups: the jerveratrum, ceveratrum, and cevanidane alkamines (Kaneko et al., 1978; Cordell 1981; figure 9). One to three atoms of oxygen distinguish the jerveratrum type (e. g., jervine, rubijervine, isorubijervine, veratramine). The group is known to occur as a mixture of free alkamines or in combination with a single molecule of D-glucose as a glucoalkaloid in unhydrolyzed plant extracts (Kupchan & Flacke 1967). Rarely these compounds occur as ester alkaloids (Shakirov & Yunusov 1980). In contrast, cerveratrum bases (e. g., zygadenine, veracevine, germinine, protoverine A) are highly hydroxylated, containing seven to nine oxygen atoms. These alkaloids often occur esterified to various acids as ester alkaloids but are seldom found as glycosides (Shakirov & Yunusov 1980). Procevine, isolated from Veratrum lobelianum (Kaneko

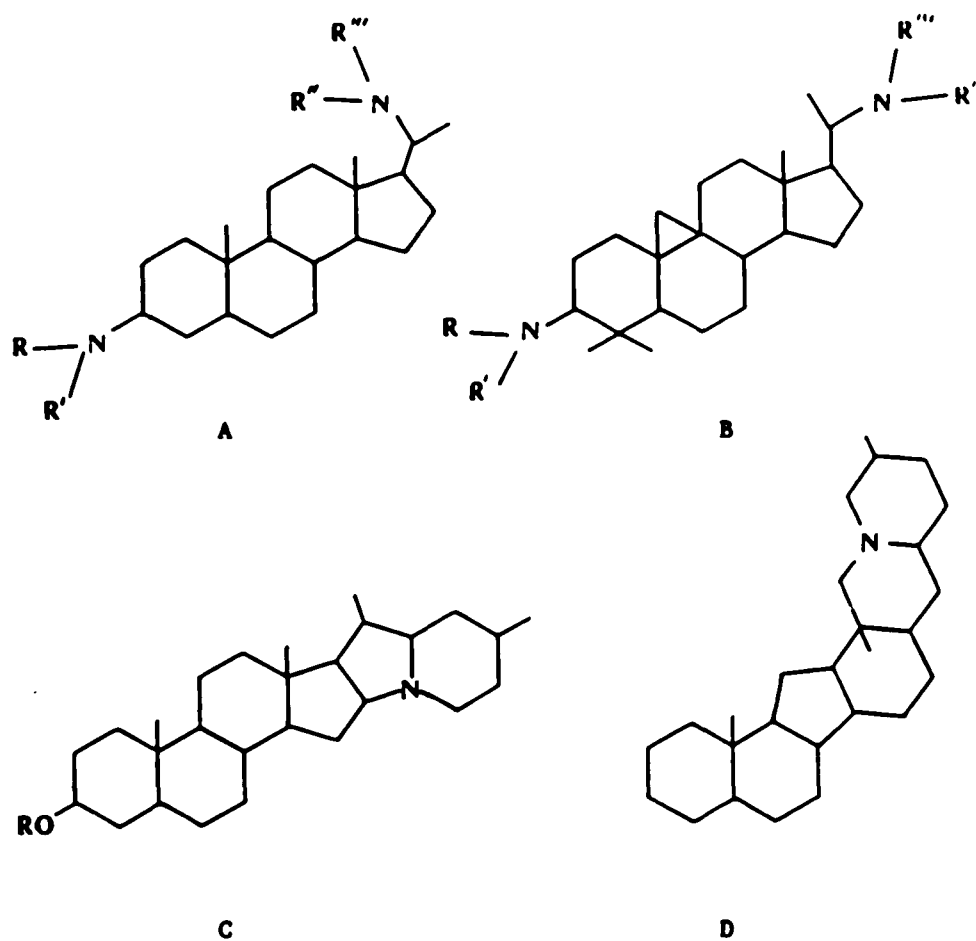


Figure 8. Examples of certain flowering plant steroidal alkaloid carbon skeletons. A, Holarrhena type (Apocynaceae); B, Buxus type (Buxaceae); C, Solanum solanidine type (Solanaceae); D, cerveratrum type (Liliaceae).

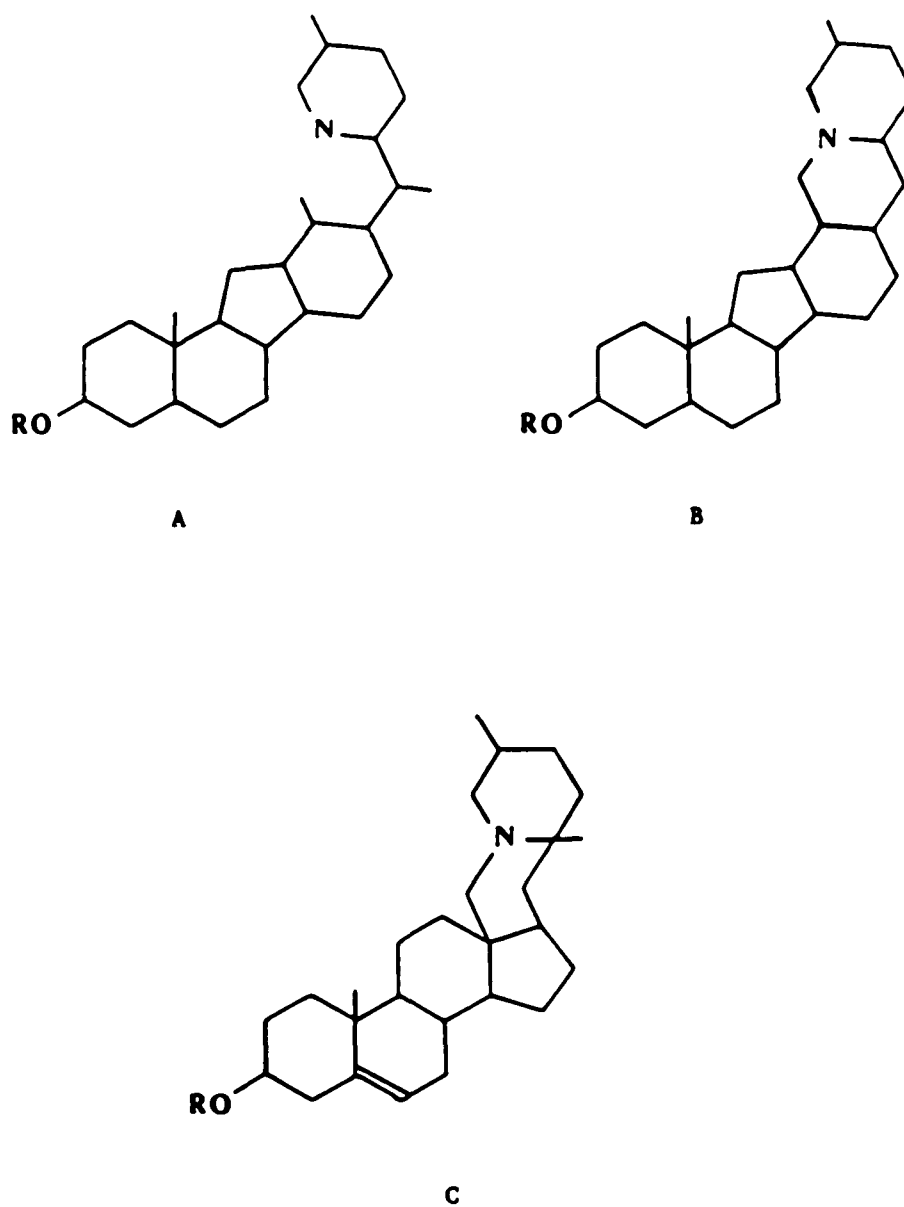


Figure 9. The three major steroidal alkaloid structural types found in the Melanthieae. A, jerveratrum; B, ceveratrum; C, cevanidane.

et al. 1978) is the first naturally occurring alkaloid identified with³⁰
a cevanidane skeleton.

The jerveratrum alkamines are potent teratogens in mammals (Keeler 1978), and the ceveratrum bases are potent antihypertensive agents as well as insecticides. As pointed out by Kupchan et al. (1961), Veratrum species possess both jerveratrum and cerveratrum alkamines, and as was more recently discovered, some even contain cevanidane alkamines. In contrast, Schoenocaulon is known to contain only cerveratrum alkamines; this is confirmed in the present study. Like Schoenocaulon, Zigadenus species are known to elaborate only cerveratrum alkamines (Kupchan et al. 1961).

The present study was undertaken to examine if the steroidal alkaloid chemistry varied quantitatively and qualitatively among Schoenocaulon species. Previous investigations of Schoenocaulon alkaloid chemistry primarily used extracts obtained from S. officinale seeds, with some little work on S. drummondii [= S. ghiesbreghtii]. All published chemical accounts used seeds of the former species. Steroidal alkaloids are not among the easiest chemical components to study because of their complexity. Indeed, this is what has prevented the alkaloid chemistry of the Melanthieae from becoming the model system for taxonomic chemical character analysis as prophesied by Kupchan et al. (1961).

Crude extracts of seeds from 12 Schoenocaulon species were studied by reverse-phase high-performance liquid chromatography (HPLC). The work was carried out under the direction of Dr. D. Strack and with the the kind help of Dr. B. Meurer-Grimes, at the Botanisches

Institut, Universität zu Köln, Köln.

Methods

Standard Extraction Procedure

The procedure used in this study is slightly modified from one mentioned in Plant Drug Analysis (Wagner et al. 1984).

Extraction:

One gram of seeds was covered with 5 ml of extraction solvent (10% ammonia in MeOH - MeOH, 1:5, v/v) and homogenized for 3 minutes. The homogenizer is cleaned with another 5 ml of extraction solvent. Both solutions were combined giving approximately 10 ml, and then stirred for 30 minutes at 60°C.

The suspension was then centrifuged at 3500 g for 10 minutes, and the supernatants were collected. Each sample's volume was determined, and then the samples were stored at -20°C in glass vials.

HPLC

HPLC analysis was carried out on a twin pump LKB system (Bromma, Sweden) connected to an UV/VIS variable wavelength detector. Injections of 20 µl were made through a Rheodyne injection system. Separations were performed on a 5 µ Nucleosil C-18 column (250 x 4 mm i.d., Macherey & Nagel, Düren, F. R. G.) using linear gradient elution from 100% solvent A (1.5% H₃PO₄, 10% CH₃CN in H₂O) to 100% solvent B (1.5% H₃PO₄, 50% CH₃CN in H₂O) at a flow rate of 1 ml/min for a 60 min cycle. Elution was detected at 230 nm (sensitivity = 0.1 a.u., and this was constant for all assays). Quantitative calculations were obtained with a Shimadzu Data Processor Chromatopac C-R3A.

UV-spectra of Standard Alkaloids
and Crude Syrup of Schoenocaulon officinale

The spectra were recorded in MeOH on a Kontron-instrument (UV/VIS) spectrophotometer and were used to determine the best wavelength for HPLC detection.

Thin Layer Chromatography

Each crude extract was chromatographed on pre-coated silica gel thin layer chromatography (TLC) plates impregnated with a fluorescent indicator (DC-Fertigplatten SILG-25UV₂₅₄; Macherey-Nagel, F.R.G.). Approximately 10 μ l of extract was applied in the form of a narrow "spot" about 1.5 cm long. The plates were developed in a solvent system of toluene-ethylacetate-diethylamine (70:20:10, v/v/v). Fluorescence at 350 nm and absorption at 254 nm were first noted on the developed plates. The plates were then sprayed with Dragendorff reagent (Wagner et al. 1984), followed by 5% NaNO₂ in H₂O. The alkaloid bands were then marked on the plate.

Results and Discussion

All Schoenocaulon species here studied contain steroidal alkaloids. The standard used in our study, β -veratrine (the kind gift of Dr. Richard Keeler), was a commercially available mixture of at least three alkaloids, two of which are known to be veratridine and cevadine (Auterhoff 1955), the third is possibly a degradation product of either of the first two. The structure of veratridine and cevadine is shown in figure 10. An HPLC profile of β -veratrine used as a standard in this study shows three major peaks with retention times of 32.8, 34.7, and 35.6 minutes (figure 11). The peak at 32.8 minutes

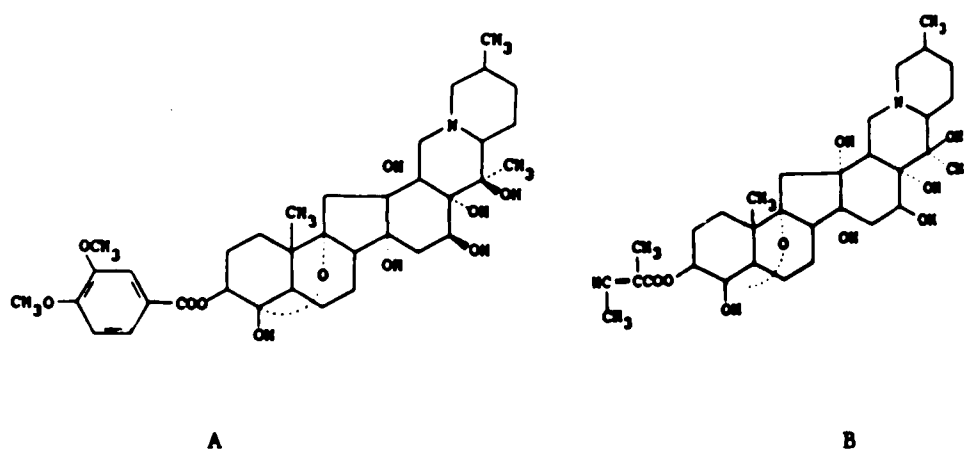


Figure 10. The chemical structure of two steroidal alkaloids from Schoenocaulon. A, veratridine; B, cevadine.

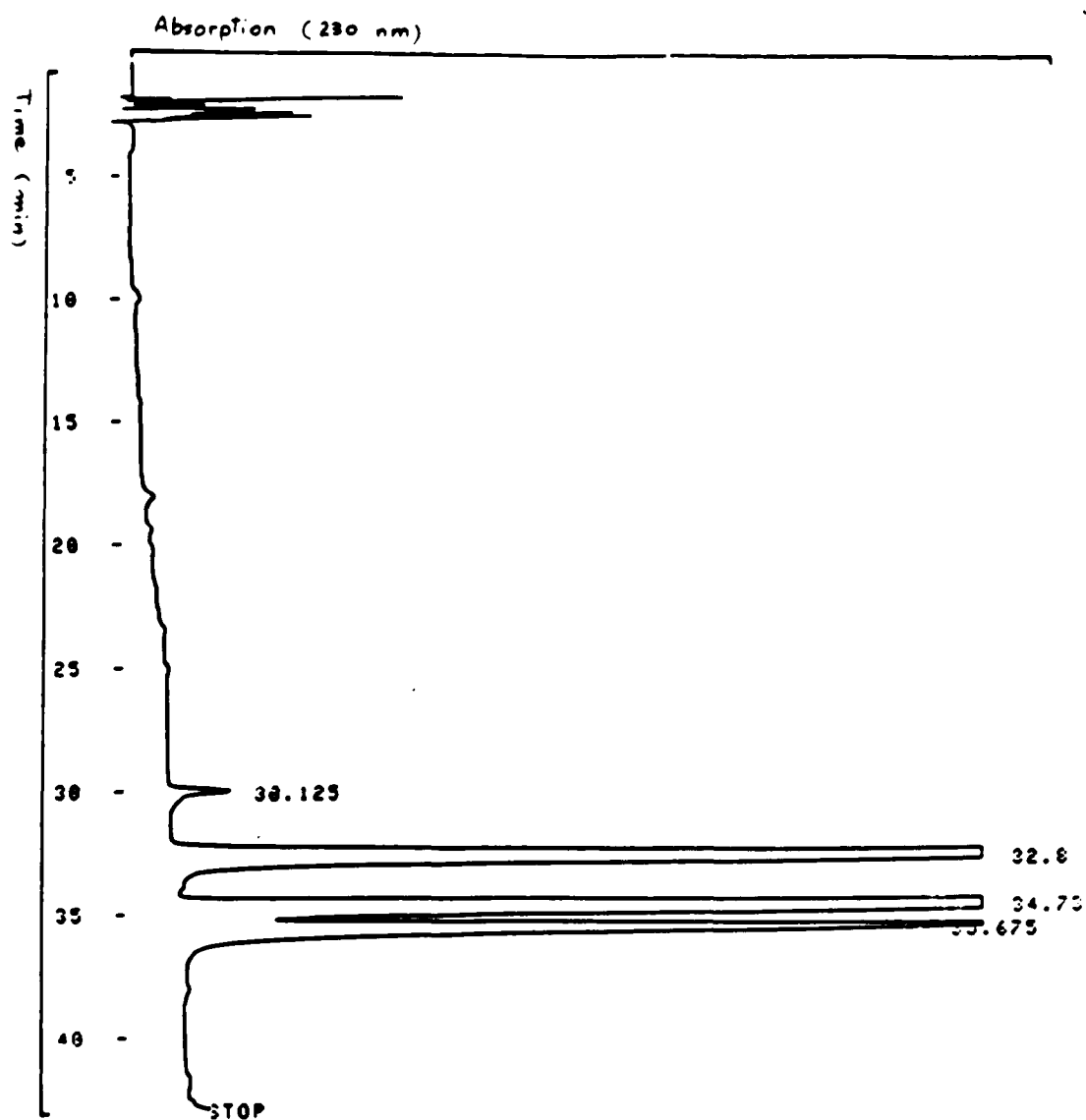


Figure 11. The HPLC profile of β -veratrine, the standard used in this study (K & K Lab, Jamaica, NY; Lot #32832S).

does not appear to be present in the chromatogram of S. officinale seed extracts (figure 12), and is believed to be the aforementioned degradation product. Peaks at 34.7 and 35.6 minutes represent veratridine and cevadine, although which chemical corresponds to which peak remains unknown.

The λ max of all the steroidal alkaloids standards we studied is ≤ 210 nm, they are detectable, however, at 220 nm and 230 nm. Concentrated crude extracts of S. officinale show a λ max of 227 nm; more dilute syrups show a λ max of ≤ 210 nm. This suggests that there are large amounts of alkaloids present in the crude syrups. There is another λ max at 320 nm, which cannot be caused by alkaloids, it may, however, indicate the presence of hydroxy-cinnamic acids in the extract (B. Meurer-Grimes, pers. comm.).

The HPLC profile of the crude syrup will first be considered as a whole. This will be followed by a short discussion on the two "veratrine" peaks. Peak positions are relative and liable to slight shifts depending upon the state of the instrument at the time of injection. This explains why retention time (R_t) is not absolute and varies slightly from analysis to analysis.

In Schoenocaulon officinale, major peaks are recorded at 34.6, 35.5, 38.2, and 40.0 minutes (figure 12). Among the many minor peaks recorded, the peaks at 41.3 and 47.3 minutes deserve attention as these minor peaks in addition to the aforementioned major ones are found to a greater or lesser degree in all species studied. Aside from the known veratrine peaks (34.7, 35.5), the aforementioned peaks possibly represent other steroidal alkaloids. Among the likely

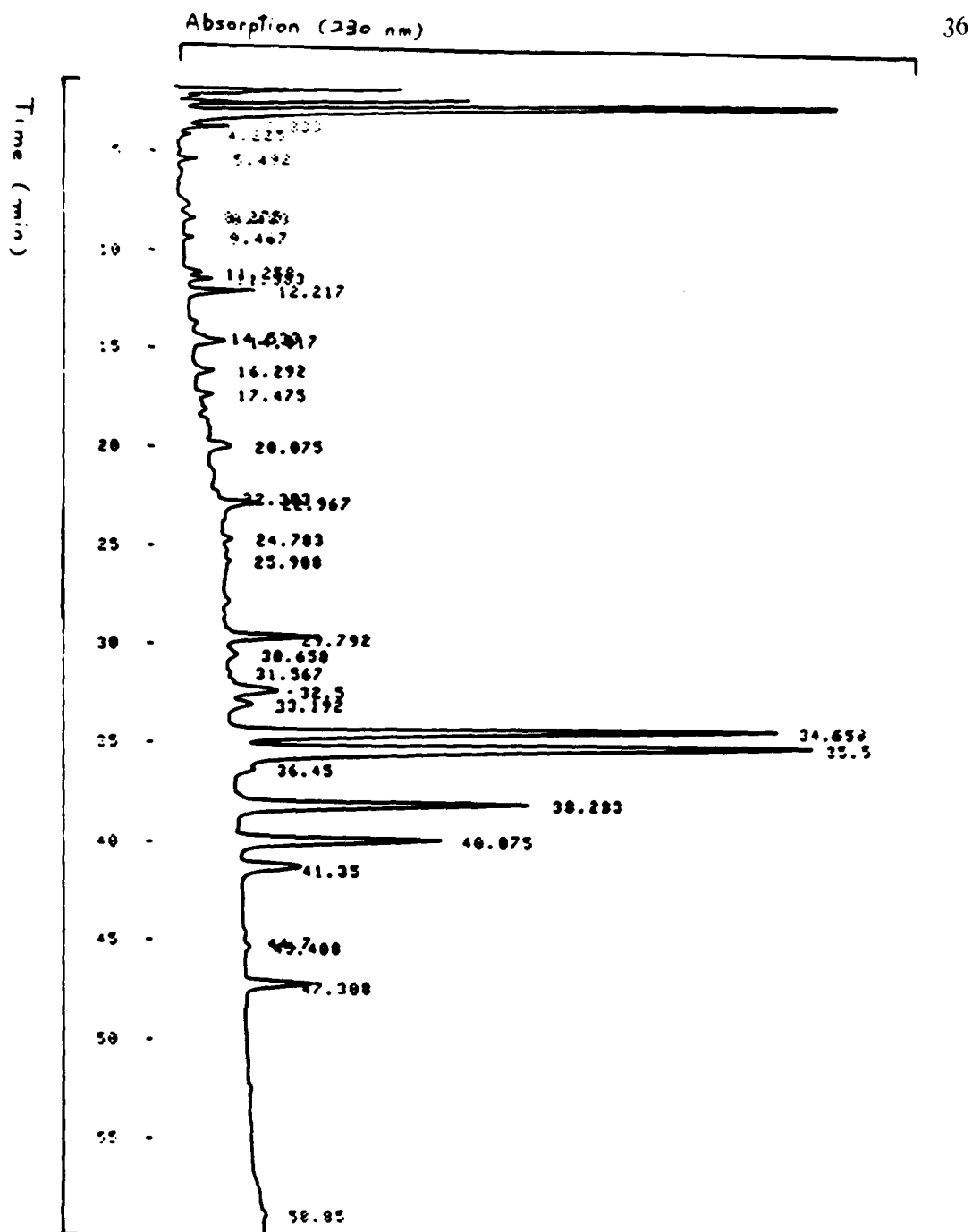


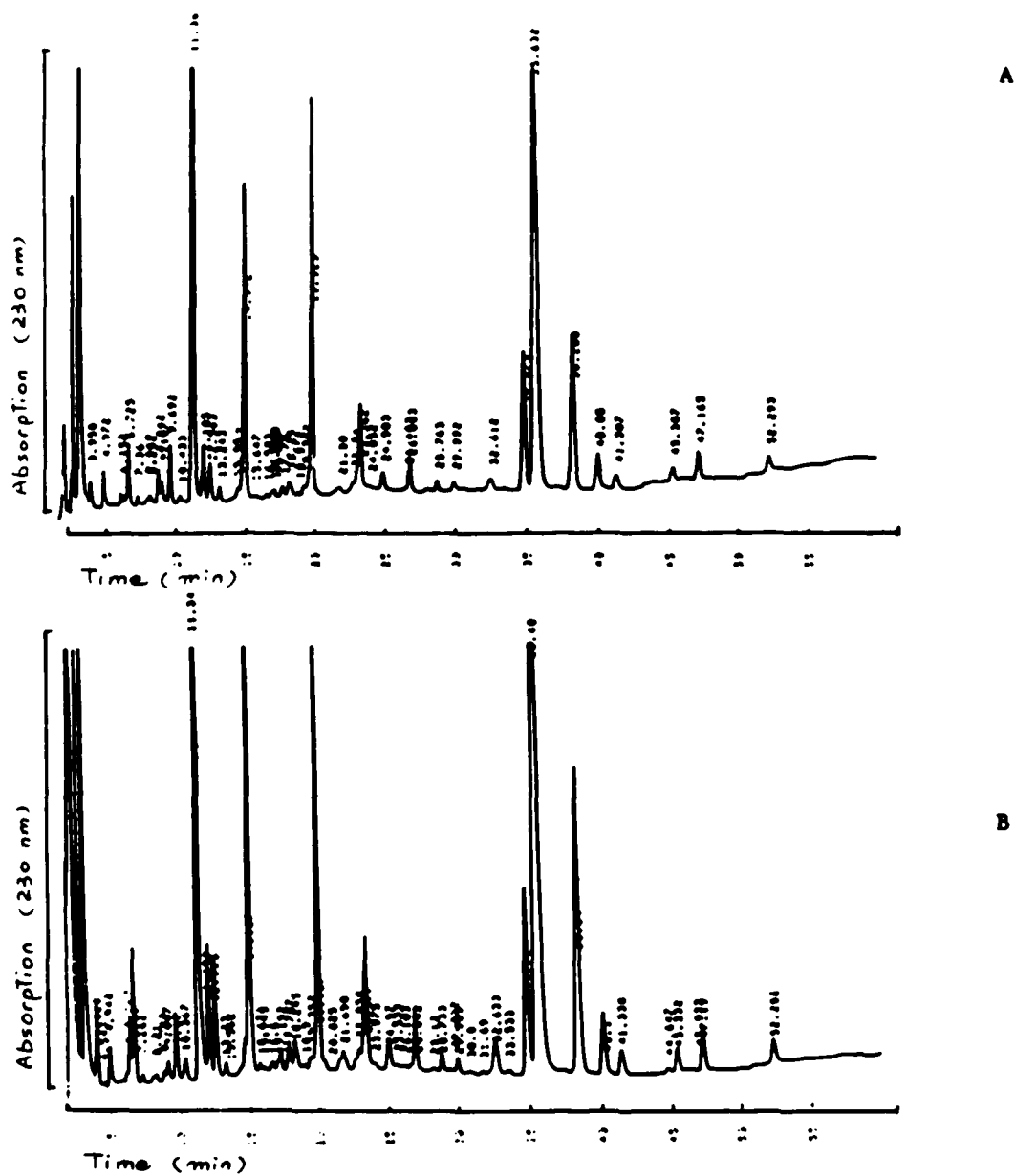
Figure 12. The HPLC profile of Schoenocaulon officinale seed extracts. [The seeds were collected from Cerro Avila near Caracas, Venezuela, and are the kind gift of Dr. A. Henderson.]

candidates are such chemicals as cevaccine, sabadinin, protocevine, sabadine, sabadillin, or cevadillin, all of which have been identified as making up the minor steroidal alkaloid fraction of S. officinale seeds (Vejdelek et al., 1956). Indeed, veratridine and cevaccine are reported as constituting approximately 90% of the total steroidal alkaloid content of S. officinale seeds (Vejdelek et al., 1956). Other minor peaks of interest are at 12.2, 23, 29.8, 32.5, and 33.2 minutes. Results from the thin layer chromatography (TLC) indicate the presence of only a few Dragendorff positive spots, i.e. alkaloids, and these had the greatest retention times. Other spots observable on the TLC plates did not migrate as far as the alkaloids, and fluoresced under ultraviolet light, a behaviour suggestive of phenolic compounds. On the basis of the forgoing results from the TLC analysis, it seems likely that the peaks with a retention time of 29.8 and above are steroidal alkaloids, but it is unlikely that the earlier peaks are. The results of spectrographic analysis of the prepared extracts do not indicate the presence of carotinoids, nor do the pigments separate into the petroleum ether phase of a petroleum ether : methanol and water phase partition system. These two facts taken together eliminate the possibility that the substances detected earlier than 29.8 minutes are carotinoids, although the observed chemistry is compatible with the hypothesis that they are anthocyanins, other flavonoids, or even substances entirely unrelated to phenolics. For this reason, although I consider the presence or absence and relative size of these earlier peaks, the taxonomic significance, if any, of the substances represented by these peaks remains unknown.

Among the control experiments conducted are two in which an extract was made from the seeds of an individual plant and from the seeds collected from various members of a single population (as was typically the source for extracts in this study). When the HPLC chromatograms for S. intermedium are compared (figure 13), it is evident that the profiles are nearly identical. The most striking difference is in the ratios of the veratrine peaks (34.9 and 35.8). In the extract from a single individual, the peak at 34.9 minutes is over twice that of the peak at 35.8, whereas in the extract from several members of the same population, the two peaks are almost equal. When the seeds from the latter were ground for twice as long as normal (see methods), the HPLC profile of the resultant extract is not significantly different (figure 13). It may be induced from the profiles of the three extracts that between members of a single population the ratios of the peaks may vary slightly and rarely considerably, but that the aspect of the profile as a whole is very similar. This phenomenon is further confirmed by the profiles of S. caldicola (figure 14).

The HPLC profiles of extracts of seeds from three different populations of S. tenuifolium growing in the Sierra de Juarez, Oaxaca, are shown in figure 15. The seeds in this instance were a little immature. When collected, they looked like large green peas. Upon desiccation, as part of specimen preparation, the seeds took on the typical Schoenocaulon seed shape and became bright orange-red. Comparison of the three different profiles illustrates several points. The first is that the different populations are chemically nearly

Figure 13. The HPLC profiles of Schoenocaulon intermedium seed extracts. A, seeds from a single plant (Frame & Tenorio 284); B, seeds from a random sample of individuals of the population; C, the same as B, but the seeds homogenized for six minutes rather than the typical three (see methods).



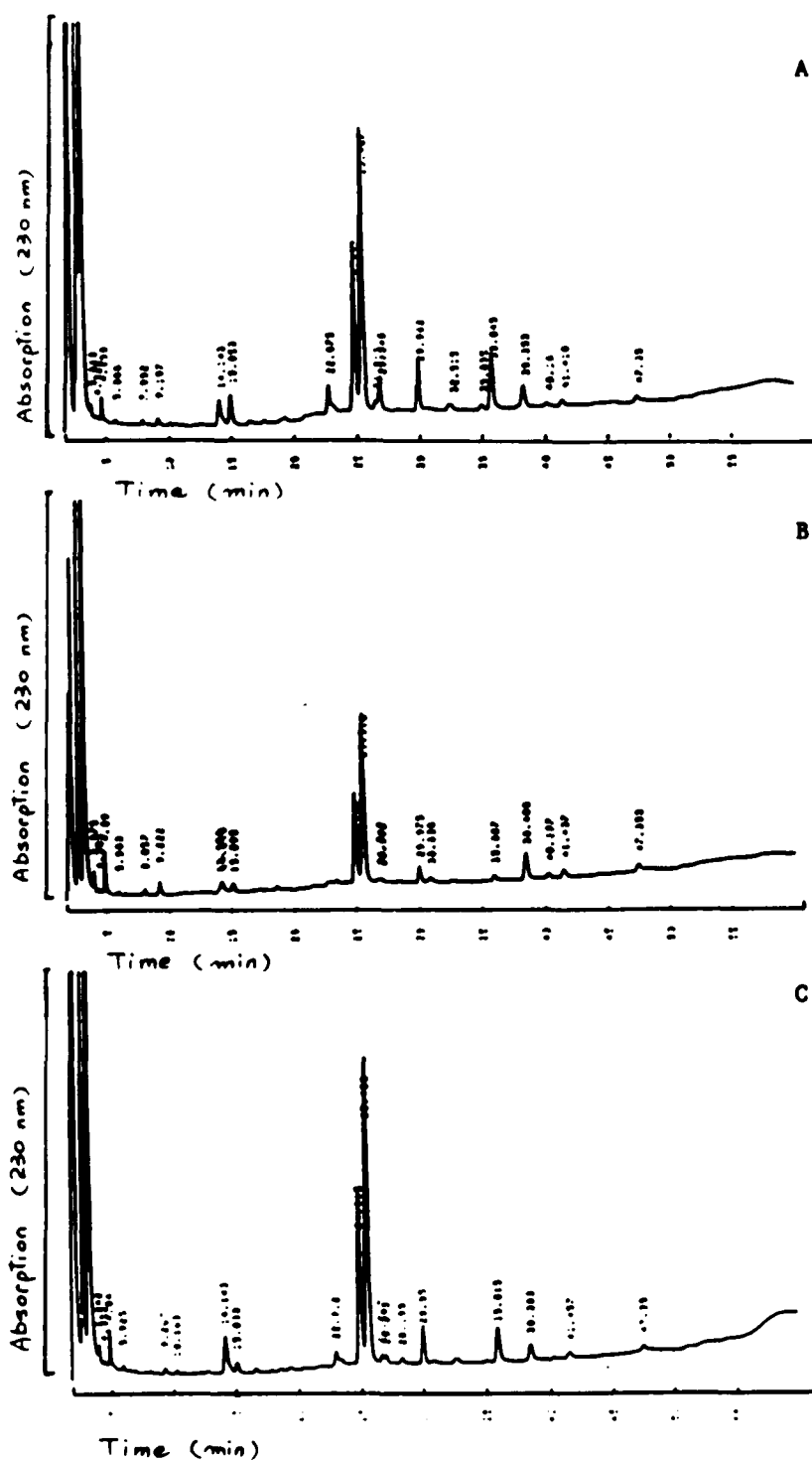


Figure 15. The HPLC profiles of the extracts of seeds from three populations of *Schoenocaulon tenuifolium*. A, Frame et al. 274; B, Frame et al. 273; C, Frame et al. 272.

identical. Another is that with the exception of major peaks at 24.8 and 25.4 minutes, the substances occur in very low quantities. This suggests that either the species accumulates only small amounts of steroidal alkaloids or else accumulation of steroidal alkaloids and other substances (as detected by our methods) occurs very late in seed maturation, possibly at the ultimate stage when the seed dehydrates.

Figure 16 shows HPLC chromatograms of two populations of S. macrocarpum, one from a rather moist habitat (Cerro Viga) and the other from a comparatively drier one (Cerro las Aguilas). The seeds from Cerro Viga were just short of completely mature, although rather more mature than the S. tenuifolium seeds mentioned above. The seeds from Cerro las Aguilas, conversely, were fully mature and of a beautiful golden brown color characteristic of the species.

Examination of the two profiles shows that the veratrine peaks are rather small and, indeed, barely distinguishable in the plants from Cerro Viga. Again, it may be that if the seeds were fully mature the peaks would be slightly larger. Yet if the population from Cerro las Aguilas is a good measure, it would appear that little more veratrine is likely to accumulate. Of course too, it may be simply that the population from Cerro Viga accumulates less veratrine than the other population. The profile of the seed extract from the Cerro las Aguilas population shows a feature common to many analyses, specifically that one of the two veratrine peaks predominates and the other is nearly lacking. Another, possibly insignificant, difference between the two populations is the presence of a large peak at 11.2 minutes found in the extract from Cerro Viga and seemingly absent in

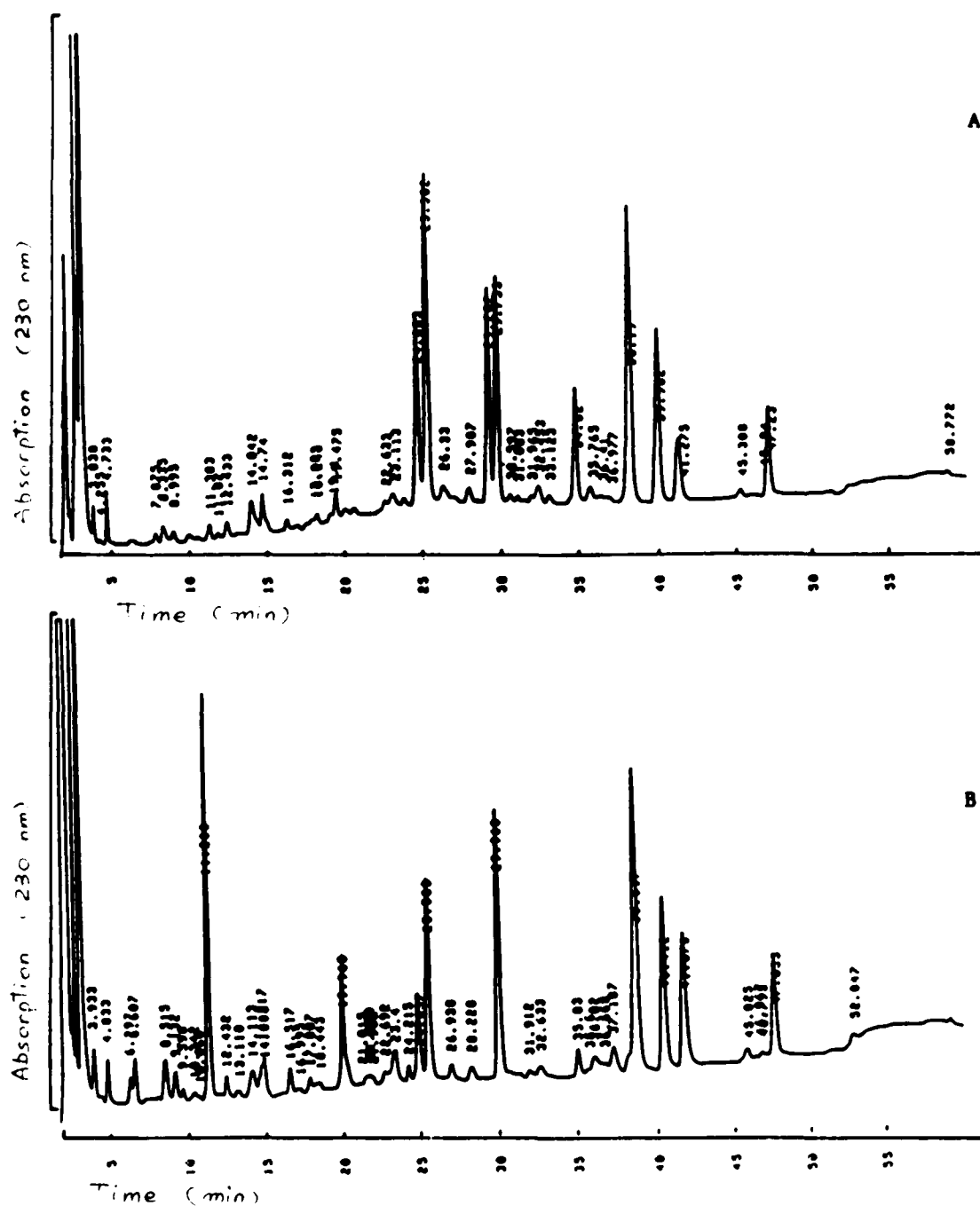
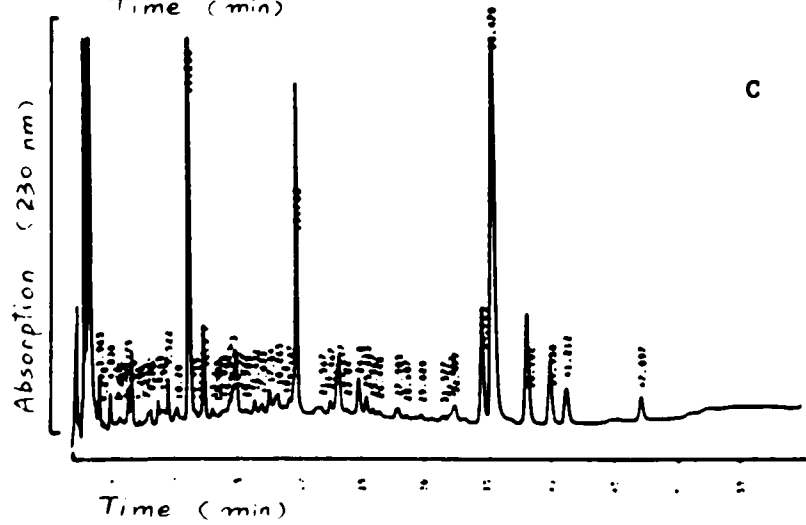
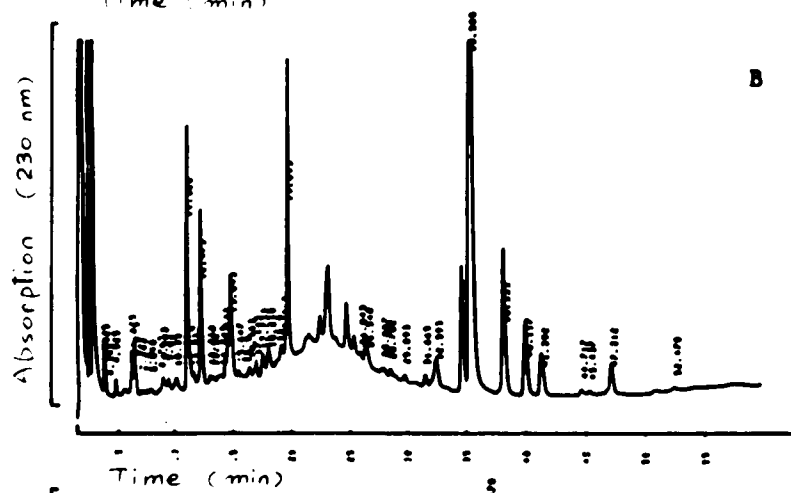
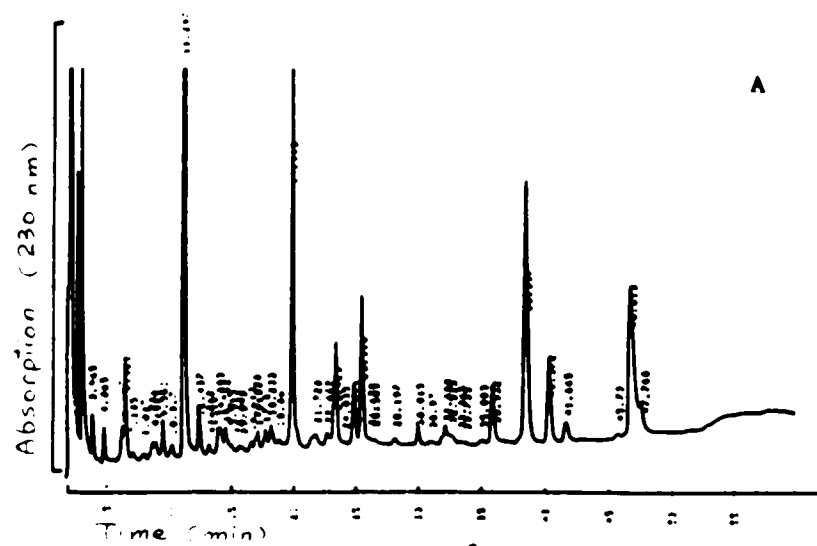


Figure 16. The HPLC profiles of Schoenocaulon macrocarpum seed extracts. A, population from Cerro las Aguilas (Frame 390); B, population from Cerro Viga (Frame 393).

the other. Similarly, a minor peak at 19.9 minutes has a match in a much smaller peak at 19.4 minutes. Another feature is that in the Cerro Viga extract a single peak is registered at 29.9 minutes, whereas two peaks at 29.2 and 29.7 minutes are found in the extract from plants growing on Cerro las Aguilas. In this example, some divergence between the populations is clearly reflected in the slight differences between the HPLC profiles. This contrasts with the previous case of S. tenuifolium, in which the profiles of different populations are quite uniform. In both cases, the HPLC profiles appear to mirror the degree of similarity between the habitats of the different populations. However, as I have no knowledge of what substances peaks with a retention time below 29.8 minutes might represent nor whether they are of any taxonomic significance, it is impossible to draw any conclusions from their variation.

The HPLC chromatograms of S. comatum provide yet another instance of the stability of steroidal alkaloids as taxonomic characters. Figure 17 shows the HPLC profiles of extracts of seeds produced in 1985 and 1986 from a single population of S. comatum which grows near San Juan Ixcaquixtla, Puebla, as well as a profile of a seed extract from a population of the same species which grows near Membrillos, Oaxaca. With the exception of some little variation in the ratios of some substances, the HPLC profile of seeds produced in 1985 is essentially identical with the profile of those produced in 1986. The dark blackish brown seeds from San Juan Ixcaquixtla were perfectly mature and the product of vigorous plants. The plants from the population near Membrillos, however, had suffered from a severe

Figure 17. The HPLC profiles of Schoenocaulon comatum seed extracts. A, population near Membrillos (Frame & Tenorio 421); B, population near San Juan Ixcaquixtla from fruit of 1986 season (Frame et al. 348); C, same population as B, from fruit of 1985 season.

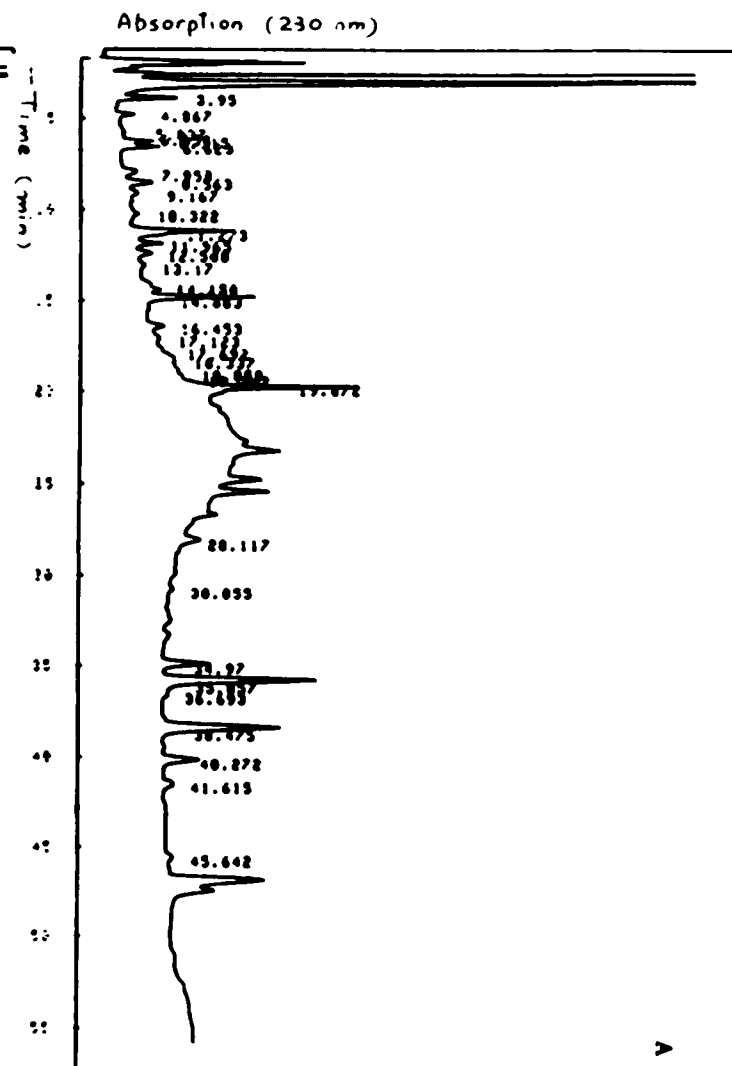


drought but had managed to set a few weak, slightly orange-colored seeds. The HPLC profiles of the seed extracts from two different populations of S. comatum are quite similar, although some differences exist. The seeds collected from near Membrillos exhibit moderate-sized peaks at 24.8 and 25.5 minutes, whereas these peaks are rather minor in the population from San Juan Ixcaquixtla; the veratrine content is very low in the seeds from near Membrillos, although not so in the other population; lastly, the seeds from near Membrillos show a moderate peak at 46.8 minutes which is absent from the extracts from the other population. Similar to the previous examples, it is possible that some populations accumulate very little veratrine as the result of natural geographic variation, or that veratrine accumulates only in the ultimate stage of seed maturation. The low veratrine content of the seeds from the population growing near Membrillos is possibly the result of the seeds never having fully matured in a biochemical sense. This is doubtless due to acute water stress which may have prematurely severed connections between the megagametophytic and the developing sporophytic tissue.

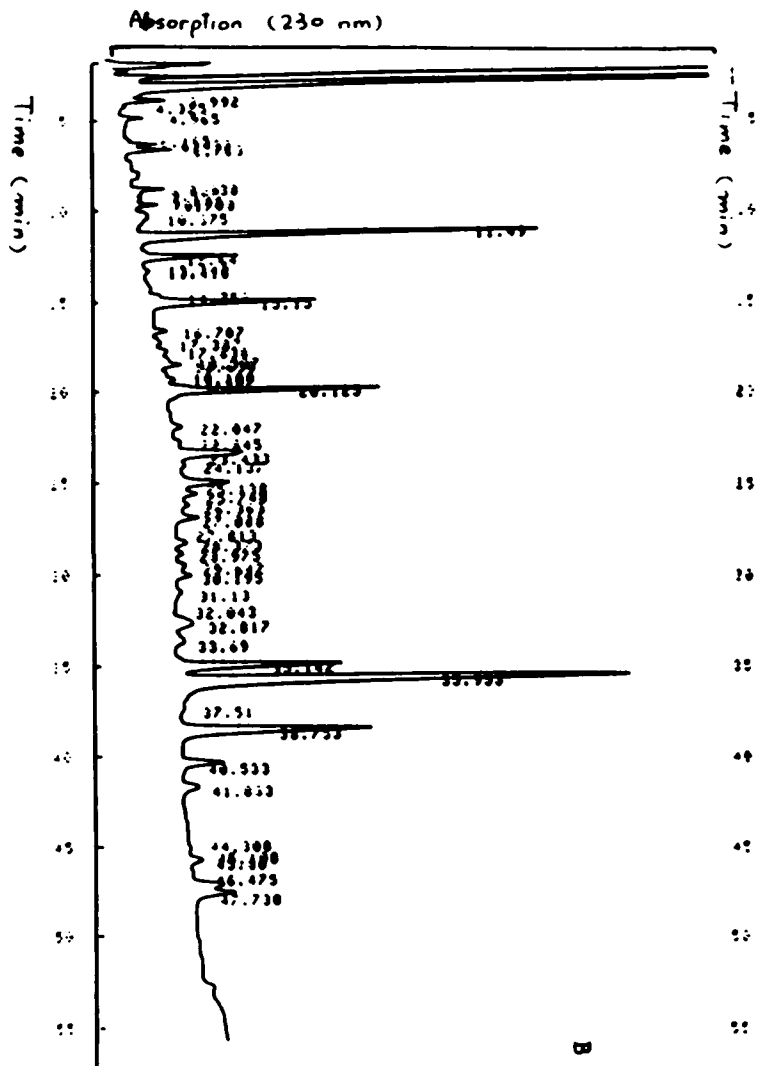
The HPLC profiles of seed extracts of two populations of S. tenorioi are shown in figure 18. The population from Cerro Verde is aberrant, at least on the grounds of morphology and relative fertility (see discussion section of S. tenorioi in chapter on taxonomic treatment). The HPLC chromatograms of the two taxa are remarkably similar, differing only in the ratios of substances, supporting my interpretation of the taxa as representing a single species. In particular, the peak at 11.4 minutes is much reduced in the seeds from

Figure 18. The HPLC profiles of Schoenocaulon tenorioi seed extracts. A, population at Cerro Verde (Frame et al. 345); B, population from near Rodeo (Frame et al. 344).

A



B



plants collected at Cerro Verde; moreover, the ratios between the peaks at 46.4 and 47.7 minutes are noticeably different.

A comparison of the HPLC chromatograms of somewhat distantly related species provides an interesting contrast to the previous examples. Figure 19 shows the HPLC profiles of the seed extracts of S. texanum and S. ghiesbreghtii. Several differences between the two are immediately apparent; the former species has a very large double peak at 14.4, and 14.6 minutes, whereas in the latter, it is very small. Moreover, there is a moderate-sized peak at 21.7 minutes which is absent from S. ghiesbreghtii extracts. S. ghiesbreghtii seed extracts show a small peak at 12.3 minutes, which is absent in S. texanum extracts. Alternately, the HPLC chromatogram of S. texanum seed extracts show a major peak at 29.6 minutes which, if present in the S. ghiesbreghtii chromatogram, is very small. The later portion of the profiles are rather similar, although the proportions of substances varies between the two species.

The HPLC chromatograms of the seed extracts of S. rzedowskii and S. megarrhizum var. megarrhizum are presented in figure 20. The profile of the first species shows a number of small- to moderate-sized peaks below 24.8 minutes that are either absent or very small in the profile of the second. The peaks at approximately 24.8 and 25.4 minutes are large in S. rzedowskii whereas in S. megarrhizum var. megarrhizum they are not. In addition, the latter species exhibits a moderate-sized peak at 29.2 minutes which is immediately followed by a major peak at 29.7 minutes. The former species essentially has only the substance represented by the peak at 29.7

Figure 19. The HPLC profiles of Schoenocaulon seed extracts. A, S. ghiesbreghtii (Frame & Geddes 265); B, S. texanum (Frame & Valdés R. 394).

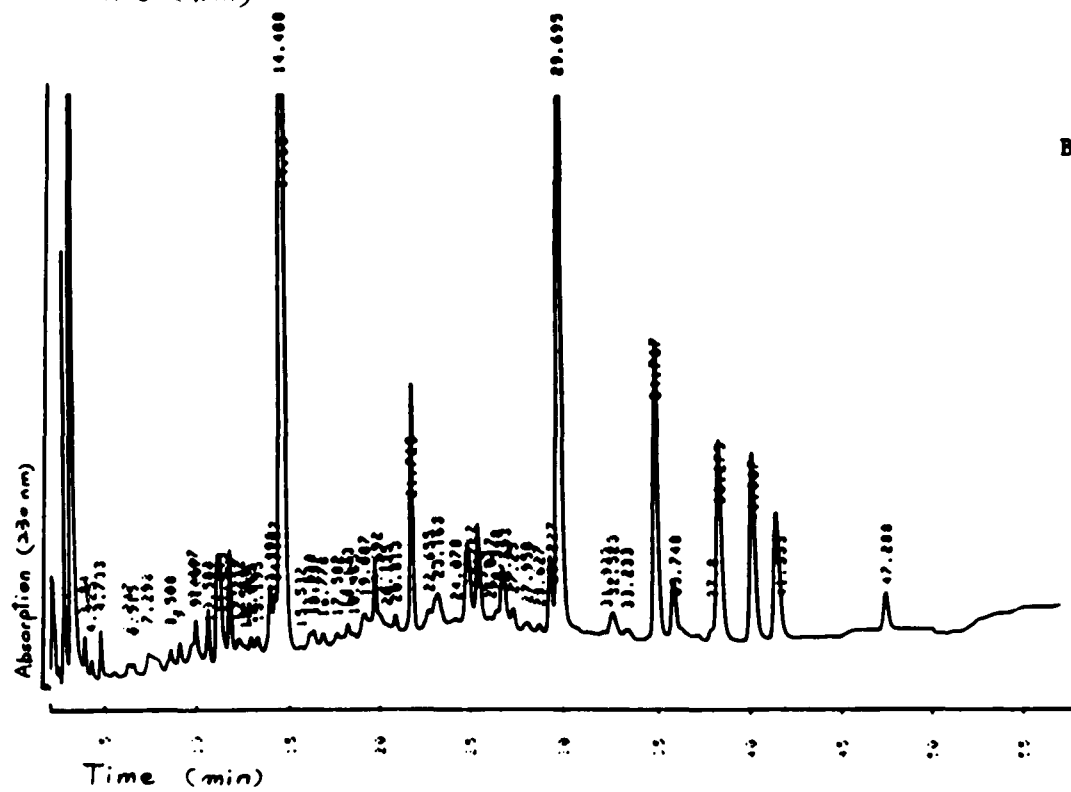
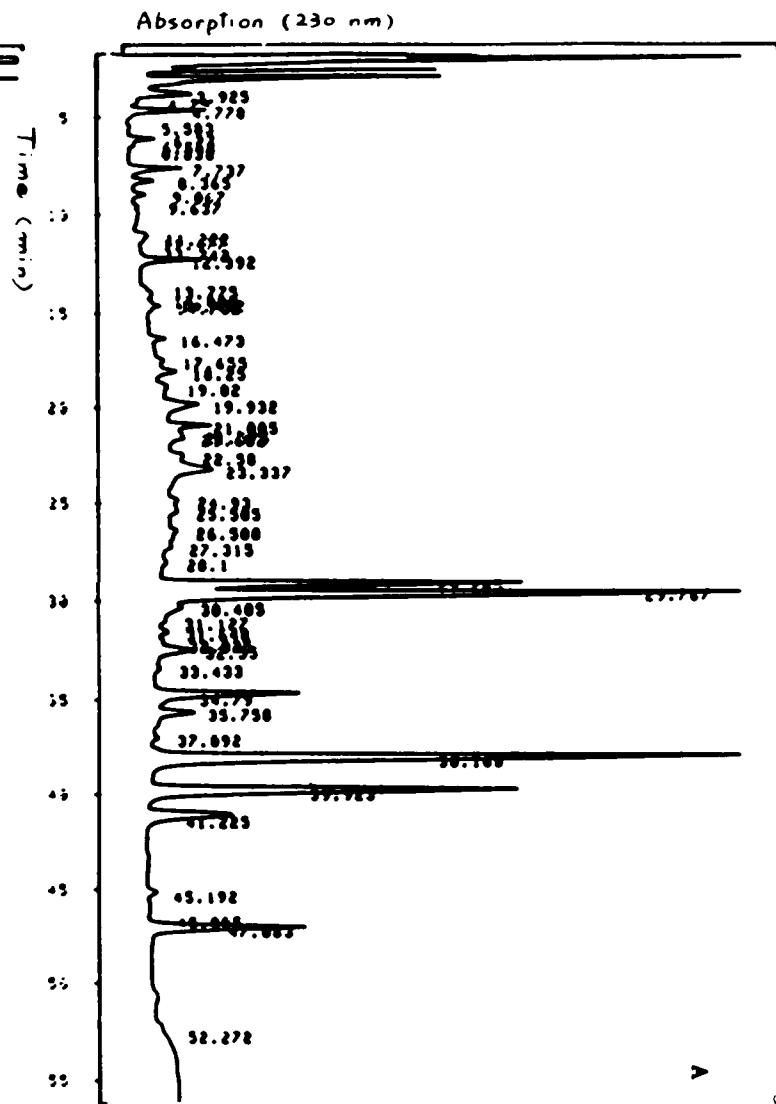
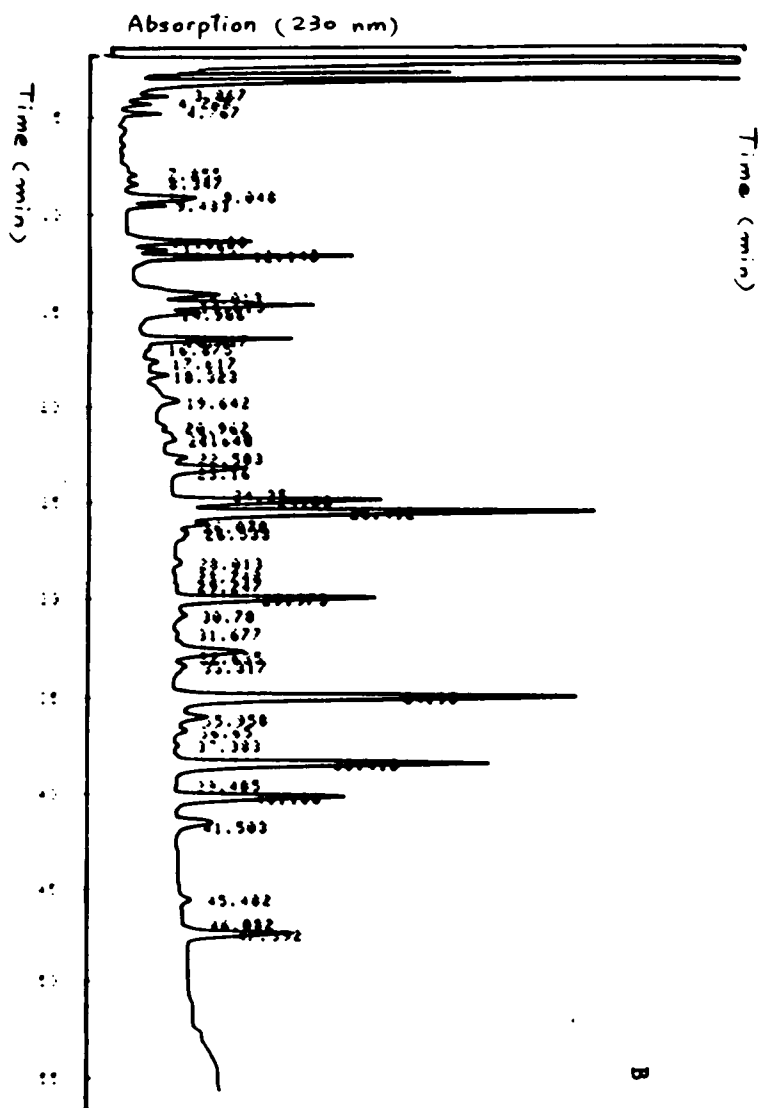


Figure 20. The HPLC profiles of Schoenocaulon seed extracts. A, S. megarrhizum var. megarrhizum (Frame & Tenorio 400); B, S. rzedowskii (Frame & Galván 245).



minutes and that in only moderate amounts. The remaining peaks are similar in the two profiles although, again, the peak proportions are different.

From the preceding chemical analyses, the following points may be gleaned regarding the chemistry of Schoenocaulon seeds:

1. Steroidal alkaloids of a population appear to be constant from year to year.
2. Steroidal alkaloid content is very similar among individuals of a population.
3. Veratridine and cevadine appear to be present in all healthy fully mature seeds.
4. Veratrine accumulation possibly occurs in the final stages of seed maturation.
6. Water-stress before the seed has reached complete maturity may possibly lead to changes in the composition of steroidal alkaloids.

By measuring the peak area of the two veratrine peaks from the different seed extracts and comparing this to the peak area of a known amount of β -veratrine, the amount of each veratrine peak and the total veratrine content of the seeds may be calculated. Table II presents the veratrine peak areas of the different seed samples. In addition, the ratio of the two veratrine peaks to each other are calculated. The relative amounts of veratridine and cevadine are quite variable, both between and within species. Table III shows the veratrine peak areas expressed as mg per gram of seeds, and the total veratrine content of each sample is calculated. The total amount of

Species and Collection #	HPLC Peak Area (PA)		Ratio of A:B
	A-34.6 min	B-35.6 min	
<i>S. calycicola</i>			
DF 274 (pop.)	659,546	3,147,348	1:4.8
<i>S. calycicola</i>			
DF 274 (individ.)	901,153	4,625,256	1:5.1
<i>S. caricifolium</i> var.			
<i>caricifolium</i> DF 283	---	1,986,988	---
<i>S. comatum</i>			
(1986) DF 348	611,595	3,085,676	1:5.1
<i>S. comatum</i>			
(1986) DF 348	781,206	4,471,608	1:5.7
<i>S. comatum*</i>			
DF 421	32,629	363,838	1:10.8
<i>S. ghiesbreghtii</i>			
DF 265	859,296	1,048,020	1:1.2
<i>S. intermedium</i>			
DF 284 (pop.)	272,134	329,893	1:1.2
<i>S. intermedium</i>			
DF 284			
(pop., 2X grind. time)	344,555	360,275	1:1.1
<i>S. intermedium</i>			
DF 284 (individ.)	630,331	238,258	2.7:1
<i>S. macrocarpum</i>			
DF 390	518,527	101,002	5.1:1
<i>S. macrocarpum**</i>			
DF 393	112,628	140,419	1:1.3
<i>S. megarrhizum</i> var.			
<i>megarrhizum</i> DF 400	541,717	145,417	3.7:1
<i>S. officinale</i>			
gift of A. Henderson	1,984,589	2,823,233	1:1.4
<i>S. rzadowskii</i>			
DF 245	1,640,057	174,140	9.4:1
<i>S. tenorioi</i>			
DF 344	679,670	2,320,861	1:3.4
<i>S. tenorioi</i>			
DF 345	172,076	649,437	1:3.8
<i>S. tenuifolium**</i>			
DF 272	---	188,784	---
<i>S. tenuifolium**</i>			
DF 273	---	31,607	---
<i>S. tenuifolium**</i>			
DF 274	---	332,255	---
<i>S. texanum</i>			
DF 394	1,078,619	197,979	5.5:1
*seeds of water-stressed plants **immature seeds			

Table II.

Seed Veratrine Content
Peak area (PA) expressed as mg/gram of seeds

Species and Collection #	PA of A	PA of B	A + B
<i>S. asclepiade</i>			
DF 274 (pop.)	3.6	17.0	20.6
<i>S. asclepiade</i>			
DF 274 (individ.)	4.9	24.9	29.8
<i>S. cariolefolium</i> var.			
<i>cariolefolium</i> DF 283	---	10.7	10.7
<i>S. oomatum</i>			
(1986) DF 348	3.3	16.6	19.9
<i>S. oomatum</i>			
(1986) DF 348	4.2	24.1	28.3
<i>S. oomatum*</i>			
DF 421	0.2	1.9	2.1
<i>S. ghiesbreghtii</i>			
DF 266	4.6	5.6	10.2
<i>S. intermedium</i>			
DF 284 (pop.)	1.6	1.8	3.3
<i>S. intermedium</i>			
DF 284			
(pop., 2X grind. time)	1.9	1.9	3.8
<i>S. intermedium</i>			
DF 284 (individ.)	3.4	1.3	4.7
<i>S. macrocarpum</i>			
DF 390	2.8	0.6	3.3
<i>S. macrocarpum**</i>			
DF 393	0.6	0.8	1.4
<i>S. megarrhizum</i> var.			
<i>megarrhizum</i> DF 400	2.9	0.8	3.7
<i>S. officinale</i>			
gift of A. Henderson	10.7	16.2	26.9
<i>S. rzadowekii</i>			
DF 246	8.8	0.9	9.7
<i>S. tenerioi</i>			
DF 344	3.7	12.6	16.2
<i>S. tenerioi</i>			
DF 346	0.9	3.6	4.4
<i>S. tenuifolium**</i>			
DF 272	---	1.0	1.0
<i>S. tenuifolium**</i>			
DF 273	---	0.2	0.2
<i>S. tenuifolium**</i>			
DF 274	---	1.8	1.8
<i>S. texanum</i>			
DF 394	6.8	1.1	6.9
Mean = 11.9	Standard deviation = 9.6		
*seeds of water-stressed plants **immature seeds			

Table III.

59
veratrine per gram of seeds varies between species, with S. calcicola,
S. comatum, and S. officinale producing the most. The first two grow
in open dry matorral habitats and this possibly relates to their
ability to accumulate what must be energy-rich chemicals. The only
obvious exception to this rule-of-thumb is S. texanum, which however,
usually grows under shrubs. That S. officinale produces large
quantities of veratrine without living in such a habitat can be
explained by its being the medicinally used species which was
doubtless bred for its ability to produce veratrine. Within species,
the total veratrine content does not tend to vary much, although, as
previously pointed out, the proportion of veratridine to cevadine may
vary considerably.

Nectar Composition

Nectar collected from two dried pressed specimens (Frame 273 and
Tenorio 14102) of Schoenocaulon tenuifolium was analyzed by Irene
Baker (unpublished). This species is unusual in the genus because it
produces copious nectar. The nectar did not appear to have been much
degraded by specimen preparation techniques. The nectar in each case
comes from a single individual plant and the two collections are from
different localities. The results of Mrs. Baker's analysis are
presented in Table IV. In both cases, sucrose is the major sugar.
The nectar appears to be unspecialized and may be consumed by any
nectar-eating insect or possibly by birds; it is not the special food
of a particular type of flower visitor. The flowers of this species,
although rather large by Schoenocaulon standards, are rather small as
compared to many other flowering plants, and are red and campanulate

Nectar Sugars

S. tenuifolium

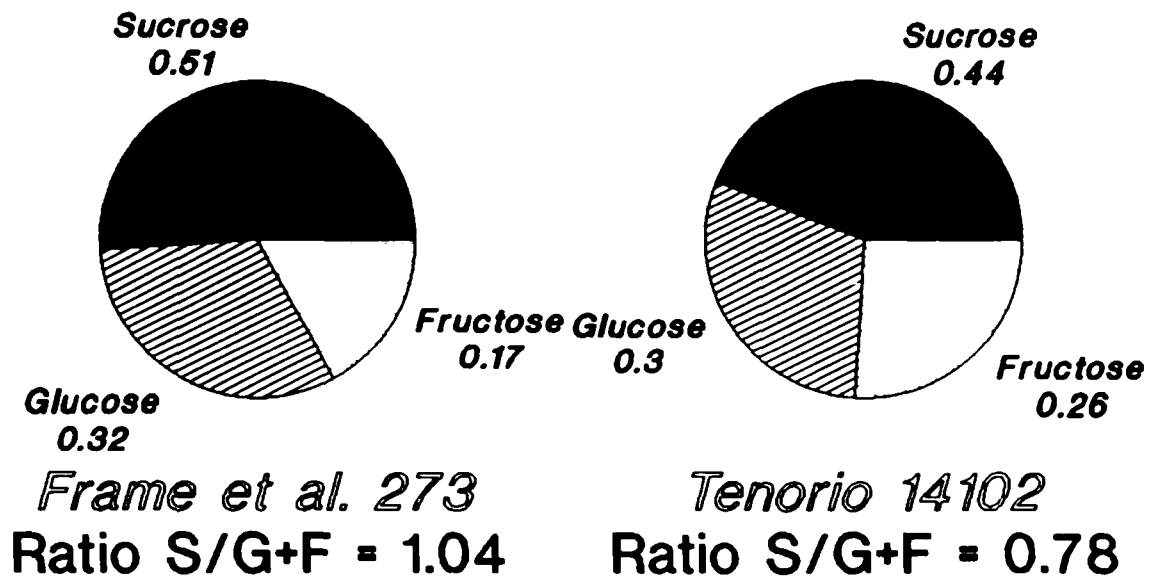


Table IV.

in outline. Notwithstanding the small flower size, it is possible that hummingbirds may be occasional visitors to S. tenuifolium flowers.

Chapter VI: Taxonomic Treatment

SCHOENOCAULON

Schoenocaulon A. Gray, Ann. Lyceum Nat. Hist. New York 4:
127-128. 1837.

Skoinlohn Rafinesque, Flora Telluriana, first part, Philadelphia.
1836. Type species. None. [nomen solum]

Veratrum subgenus Sabadilla Brandt & Ratzeburg, in Hayne, Getreue
Darstellung und Beschreibung der in der Arzneykunde gebräuchlichen
Gewächse. Vol. 13. t. 27. Auf Kosten der Verfasser, Berlin. 1837.

Type species: Veratrum officinale Brandt & Ratzeburg.

Sabadilla Schlecht., Linnaea 18: 444. 1844.

Asagraea Lindley, Edward's Bot. Reg. 2: t 33. 1839. Type
species Asagraea officinalis Lindley.

Original description

FLORES hermaphroditi. PERIANTHII foliola herbacea
(lineari-oblonga, obtusa), basi vix coalita, suberecta, exungiculata,
eglandulosa. STAMINA 6; filamentis subulatis cum perianthio insertis,
eodemque demum duplo longioribus. ANTHERAE (magnae) regiformes
(loculis apice connatis et confluentibus), post dehiscentiam
clypeolatae. OVARIA 3, angulis internis concreta, 6-8 ovulata, stylis
perbrevibus sensim apiculata: stigmata simplicia minuta. CAPSULA
.....

CAULIS bulbus tunicatus: folia omnia radicalia, caricina,
praelonga et angustissima, arida subcanaliculata: scapus
simplicissimus, pergracilis, prorsus nudus: flores parvi, arcte
sessiles (singuli bractea minuta stipati), in spicam gracilem

dispositi.

Updated description

Perennial scapose herbs with tunicated bulbs, proliferating by means of an often truncated woody rhizome; leaves narrow, grasslike, conduplicate as they emerge from the neck of a fibrous tunic; scapes simple, terete to often flattened basally, each individual bulb producing 1 or rarely 2; inflorescence a spikelike raceme, the perfect flowers sessile to pedicelled when the pollen is first being shed, usually becoming pedicelled as the ovary matures, each subtended by a persistent, membranous to slightly fleshy, transversely broadly ovate, generally erose-margined bract, this surrounding and partly enclosing the bud, reflexed in fruit; axis elongating as the flowers mature, the uppermost bracts empty or concealing rudimentary flowers; tepals 6, free to rarely slightly basally connate, linear to broadly ovate, red, magenta-green, cream, green, green-cream, green-yellow, green-pink, green-purple, bluish green, purple, or purple-brown, usually with a hyaline or rarely slightly herbaceous auricle, withering-persistent; perigonal nectaries at tepal base mostly poorly-developed and forming a depression or pit, or rarely well-developed and forming distinctive pads; stamens 6, free from the tepals; filaments when pollen is being shed subulate to proximally linear and distally dilated, when dry their 1 nerve appearing as a median ridge, rarely basally adanate to a short column below the ovary; anthers reniform, basifixed, extrorse, explanate after dehiscence; pollen monocolpate or monocolpate with an operculum, brilliant yellow; ovary superior, rarely raised with the filaments on a short column above the perianth, 3-locular, the locules

sometimes barely coherent; ovules 2-16 in each locule; placentation essentially axile; styles 3, free, persistent; stigmas hardly differentiated and merely a continuation of the styles; fruit a 3-locular septicidal capsule, 1 or rarely 2 locules sometimes rudimentary; seeds 1-8 in each locule, ellipsoid to ovoid, irregularly compressed or angled by mutual pressure, rugose to striate, containing copious endosperm.

Type species. Schoenocaulon gracile A. Gray [Schoenocaulon dubium (Michx.) Small].

The name of the genus derives from the Greek, schoenos, rush + caulos, stem, referring to the naked scape.

Distribution. A genus of 24 species, mostly endemic to Mexico, two extending north into Texas one of which just reaches New Mexico, one extending south to Peru and Venezuela, and one confined to Florida.

Herbarium acronyms used in this treatment follow Holmgren et al. (1981).

How to use the key to species

This key has been designed for use with fresh or boiled flowers. Schoenocaulon flowers rehydrate wonderfully well, although any purple pigment will be destroyed by this treatment (as also by excessive dry heat) so color must be noted beforehand. All measurements given in this key are taken from boiled flowers. Dehydrated flowers and pedicels are somewhat smaller as a result of shrinkage. It is best to just get into the habit of detaching a mature flower (how to tell maturity is discussed below) by its pedicel from the scape, boiling it, and then taking measurements. If this regimen is not adhered to, I can guarantee little success with this key.

The anthers open hydrostatically and for this reason, when a flower is boiled the previously open anthers become closed. So too, on dried pressed specimens, many anthers are prematurely open as a result of the desiccation necessary for specimen preparation. In nature the anthers do not dehisce until they are at least equal with the tepals and usually when they are about 1.5 times the length of the tepals. When selecting a mature flower, look for one in which the filaments have elongated but to which the dehiscing anthers are still attached; moreover flowers at this stage should be just distal to flowers in which the anthers have abscised. It is also important that one consider the state of the inflorescence. If it is just coming into flower, the inflorescence will appear condensed whether or not it will ultimately be so. Close inspection of the lowermost flowers should give some clue to how much expansion between flowers will ultimately take place. If possible, it is best to examine

flowers which come from the lower to middle portion of the inflorescence, as the uppermost are often staminate and sometimes smaller overall.

The leaves of Schoenocaulon are plicate as they emerge from the neck of the tunic, and often remain folded much of their life. It is often difficult to find fully open leaves on specimens, especially on those species which live in xeric habitats, but upon close inspection some places along the leaf are usually seen to be fully expanded.

Key to species.

1. Tepals red to red-green or magenta-green; flowers campanulate in outline. 1. S. tenuifolium.
1. Tepals cream, green, green-cream, green-yellow, green-pink, green-purple, bluish green, purple, or purple-brown, flowers not campanulate.
 2. Tepals cream.
 3. Perigonal nectaries well-developed, appearing as thick pads at tepal base; tepals fleshy and opaque. 2. S. officinale.
 3. Perigonal nectaries poorly-developed, appearing as shiny nectariferous tissue at tepal base; tepals petaloid to slightly fleshy and usually translucent. 3. S. pellucidum.
 2. Tepals green, green-cream, green-yellow, green-pink, green-purple, bluish green, purple or purple-brown.
 4. Tepal margin undulate to crenulate or minutely denticulate, auricles essentially lacking; tepals often nearly petaloid.
 5. Filaments at least twice the length of the tepals, usually dilated above, widespead. 4. S. ghiesbreghtii.
 5. Filaments 1.5 times the length of the tepals, subulate.

Endemic to the Sierra del Tigre, in south-central Jalisco.
 5. S. tigrense.
 4. Blade margin entire, auricles usually present and margin variable from entire to crenulate; tepals usually slightly fleshy to fleshy.
 6. Tepals dark purple, or purple-brown sometimes only so proximally; if perianth faded and appearing green-brown,

the tepals usually with a single median vein and the auricle margin crenate.

7. Filaments at maturity just surpassing tepals. Endemic to regions of exposed granite outcrops north of

Pachuca, Hidalgo.

6. S. obtusum.

7. Filaments at maturity about 1.5 times the length of the tepals.

8. Tepals purple, fleshy, and with indistinct auricles which form raised lateral edges of basal channel.

7. S. intermedium.

8. Tepals purple to purple-brown, mostly herbaceous to proximally slightly fleshy, auricles distinct to nearly lacking.

9. Tepals distinctly auriculate, the auricle margin usually crenulate. Tunic neck tapering (often abruptly) to 3-7 mm in diameter as it approaches soil surface. Endemic to the open pine forests of the Sierra de Agua de Afuera and adjacent heights in the Sierrra Madre Oriental of Nuevo León and Tamalipas.

8. S. ignigenum.

9. Tepals auriculate to barely so, the auricle margin not noticeably crenulate. Tunic neck not tapering significantly as it approaches soil surface, fairly widespread.

9. S. plumosum.

6. Tepals green, green-cream, green-yellow, green-purple, or bluish-purple; mostly 3-veined, auricle margin entire to crenate.

10. Inflorescence loose, the flowers well-separated from each other along the inflorescence axis.

11. Plants of very small stature, the inflorescence axis at most 30 cm long; bulb-fibers papery to fine.

12. Leaves 14-24 cm long. Tepals with poorly-developed auricles. Capsules plumply ellipsoid to globose, not appressed to inflorescence axis. Puebla and Oaxaca.

10. S. tenorioi.

12. Leaves 30-45 cm long. Tepals with well-developed auricles. Capsules ovoid to ellipsoid, appressed to inflorescence axis. Endemic to the volcanic hills in the region of Tepoztlán, Morelos.

11. S. tenue.

11. Plants of small to relatively large stature, inflorescence axis greater than 30 cm long, or if shorter then bulb-fibers very coarse.

13. Plants very robust, filaments at maturity 7.3-8 mm long. Endemic to Cerro San Felipe, Oaxaca.

12. S. konzattii.

13. Plants generally less robust, filaments at maturity no more than 6.2 mm, or rarely the

plants robust and the filaments to 7 mm at maturity.

14. Plants with coarse horsehair-like bulb-fibers; inflorescence attenuate and approximately equalling the scape in length.

13. S. comatum.

14. Plants with papery to coarse bulb-fibers; inflorescence not attenuate, or if rarely the bulb-fibers very coarse and the inflorescence attenuate, then the scape much longer than the inflorescence.

15. Flowers distinctly pedicellate when pollen is first being shed, the pedicels at least 0.6 mm long.

16. Unopened anthers green; tepals bluish green to green-purple; ovary green, later green-purple.

14. S. jaliscense.

16. Unopened anthers yellow to peach or peach-purple; tepals green to green-cream or green-purple; ovary white, later pink to pink-purple.

17. Pedicels strongly curving to orient capsules close, and becoming slightly appressed, to inflorescence axis. Scape very sturdy and plants appearing somewhat coarse.

18. Tepals distally spreading, green.

15. S. megarrhizum.

18. Tepals not spreading, green-cream.

3. S. pellucidum.

17. Capsules not appressed to inflorescence axis nor pedicels strongly curving. Scape flexuous when young, plants appearing long and delicate.

16. S. calcicola.

15. Flowers sessile to subsessile when pollen is first being shed, the pedicels when present no more than 0.6 mm long.

19. Flowers strictly sessile when pollen is first being shed.

20. Tepals green. Bulb enveloped underground by layers of papery leaf bases. Endemic to the dry pinelands and sandhills of Florida.

17. S. dubium.

20. Tepals bluish green to green-purple. Bulb enveloped underground by a tunic of fine fibers. Jalisco and San Luis Potosí.

14. S. jaliscense.

19. Flowers subsessile when pollen is first being shed, the pedicels no more than 0.6 mm long.

21. Inflorescence attenuate, uppermost flowers minute. Scape at least 53 cm and very

slender. Endemic to the dry pinelands and sandhills of Florida. 17. S. dubium.

21. Inflorescence not noticeably attenuate, or if so then the uppermost flowers not minute nor scape thick. Scape less than 53 cm long, or if rarely longer, then thick (at least at base).

22. Tepals with indistinct auricles and which form raised edges to the basal channel. Carpels loosely sealed. Immature capsules often brilliant magenta-purple.

9. S. intermedium.

22. Tepals distinctly auriculate. Carpels well-sealed. Immature capsules generally green to green-purple, or rarely purple-green.

23. Tepals distally spreading; inflorescence very loose. Scape long and slender. Small plumply ellipsoid to globose capsules not appressed to inflorescence axis.

16. S. calcicola.

23. Tepals not distally spreading; inflorescence moderately loose. Scape varying from long,

relatively thick and slightly
tapering to distinctly stout and
hardly tapering. Capsules various
and appressed to inflorescence
axis.

24. Scape relatively thick,
at least at base, and
tapering. Plants tall and
robust or rarely relatively
short, and the inflorescence
attenuate. Tepals not
channeled along their length.

18. S. mortonii.

24. In fruit the scape distinctly
stout and hardly tapering.
Plants relatively short.
Inflorescence not attenuate.
Tepals adaxially canaliculate
with 2-3 channels.

19. S. rzedowskii.

10. Inflorescence moderately condensed to very condensed, the
flowers crowded along the inflorescence axis.

25. Inflorescence relatively short and comparatively
few-flowered, no more than 12 cm long with up to 65
flowers.

26. Inflorescence very condensed, with nearly no

expansion between the green to green-yellow flowers, and forming a distinctly 5-ranked tight spiral. Stamens just emergent. Endemic to the Pine-tussock grass communities of the Transverse Volcanic Belt.

20. S. pringlei.

26. Inflorescence condensed, but generally with a little expansion between the flowers, and a spiral not readily discernable. Filaments at least 1.5 times the length of the tepals.

27. Scape relatively short, no more than 30 cm long, rarely to 42 cm but then very stout and hardly tapering. Inflorescence slightly condensed to condensed.

28. Fruits appearing inflated, plumply ellipsoid to globose and not closely appressed to inflorescence axis. Mature filaments white to pale pink.

21. S. caricifolium.

28. Fruits generally not inflated, or if so then ellipsoid to plumply ellipsoid and closely appressed to inflorescence axis. Mature filaments usually bright magenta.

29. Tepals distinctly auriculate, and adaxially canaliculate with 2-3 channels. Inflorescence only slightly condensed. When in fruit, scape very

stout and hardly tapering.

19. S. rzedowskii.

29. Tepals with or without auricles, but never adaxially canaliculate with 2-3 channels. Inflorescence condensed. When in fruit, scape usually tapering often from a moderately thick base.

22. S. texanum.

27. Scape relatively long, at least 35 cm, and gently tapering. Inflorescence condensed.
30. Flowers brightly colored, uppermost one-third to one-half functionally staminate. Immature to mature capsule usually raised with the filaments above the perianth. Inflorescence often flexuous. Leaves generally many and long, 6-11 and 47-125 cm long.

9. S. plumosum.

30. Flowers usually not very brightly colored, usually only uppermost 1-12 flowers functionally staminate, rarely more if flowers withered. Immature to mature capsule rarely raised with the filaments above the perianth, usually only so if flowers withered or ovules aborted. Inflorescence usually erect. Leaves usually few and relatively short, (3-) 5-8 and 15-60 cm long.

22. S. texanum.

25. Inflorescence relatively long and many-flowered, usually

at least 12 cm long with more than 65 flowers.

31. Leaves relatively wide and pliant, mostly 7-10.5 mm wide. Pedicels of immature to mature capsules noticeably long and thin, 3-4.5 mm long and 1-1.5 mm in diameter. Flowers usually producing copious nectar.

23. S. madidorum.

31. Leaves wide or narrow, but if relatively wide not soft and pliant. Pedicels of immature to mature capsules mostly less than 3 mm, or if longer than the tepals pale green-cream. Flowers not producing copious nectar.

32. Tepals pale green to green-cream. Scape quite thick and at least a meter long.

3. S. pellucidum.

32. Tepals green to green-purple, or if pale green then scape much less than a meter tall.
33. When pollen is first being shed, tepals at least 3 mm long. The bulb shallowly to deeply buried. If deeply buried then the immature to mature capsule raised with the filaments above the perianth.
34. Tepals distinctly long and narrow, often with barely discernable auricles. Immature to mature capsule raised with the filaments above the perianth. Plants mostly robust with many broad leaves.

Inflorescence condensed.

24. S. macrocarpum.

34. Tepals various, but not strikingly narrow, and often distinctly auriculate. Immature to mature capsule only very rarely raised with the filaments above the perianth, usually only so if flowers withered or ovules aborted. Plants relatively small to rarely large and robust, leaves mostly relatively few and narrow. Inflorescence slightly condensed to condensed.

35. Tepals distinctly auriculate, and adaxially canaliculate with 2-3 channels. Inflorescence only slightly condensed. When in fruit, scape very stout and hardly tapering.

21. S. rzedowskii.

35. Tepals with or without auricles, but never adaxially canaliculate with 2-3 channels. Inflorescence condensed. When in fruit, scape usually tapering often from a moderately thick base.

22. S. texanum.

33. When pollen is first being shed, tepals usually less than 3 mm long, or if slightly

longer, the bulb deeply buried and the
immature to mature capsule not raised with the
filaments above the perianth.

36. Immature to mature capsule usually raised
with the filaments above the perianth.

Bulb usually shallowly buried.

Inflorescence condensed. Limestone soils.

9. S. plumosum.

36. Immature to mature capsule not raised with
the filaments above the perianth. Bulb
usually deeply-buried. Inflorescence
slightly condensed. Volcanic soils.

18. S. mertonii.

1. *Schoenocaulon tenuifolium* (Mart. & Gal.) Robins. & Greenm., Amer. J. Sci, Ser III. 50: 168. 1895. **Type:** MEXICO. Oaxaca: "Terre froide à 8-10000-, Cordillera." (Galeotti 5585, BR, the holotype). *Veratrum tenuifolium* Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 9(2): 380-381. 1842. *Asagraea? tenuifolia* Kunth, Enum. Pl. 700. 1843.

Figure 21 & 22.

Bulb ovoid to spherical or transversely ellipsoid, 2.3-6 (-7) cm long and 2-5 cm in diameter, enveloped underground by a tunic of dark brown papery bulb scales to coarse fibers, these forming a neck 9-28 cm long and 1-2.7 (-4) cm in diameter of moderately to very coarse dark brown fibers, the truncated woody rhizome often appressed to the bulb; leaves 8-12, sometimes emerging with inflorescence, when mature 45-150 cm long and 3.3-11 mm wide, 2-3 times the length of the scape, green, 5-16-nerved, the nerves spaced 0.4-1 mm apart; scape 11-40 cm long and 1.6-5 mm in diameter, red-purple, the slightly to very condensed 45-120-flowered raceme (6.5-) 9.5-18 cm long; flowers 4-5-ranked, when pollen is first being shed sessile to subsessile, the pedicels no more than 0.3 mm long, the uppermost 3-50 flowers functionally staminate, the uppermost 20-40 bracts empty or concealing rudimentary flowers forming a round to almost narrow crown; bracts irregularly pentagonal, 2.5-4.5 mm long and 3.5-5 mm wide, pale green to red-brown, translucent, the veins 6-8, wine-colored, the margin denticulate to erose; the pedicels of nearly mature to mature capsules ascending 30-45° from stem, 1-2 mm long and 1.2-2.2 mm in diameter; those of any vertical rank 1-1.5 cm apart; tepals when

pollen is first being shed 2.5-5.5 mm long, obovate to nearly spherical or falciform in outline, petaloid, greenish-red to red-purple, margin entire to minutely denticulate or erose, divisions often confined to barely perceptible auricles, at base canaliculate and 0.8-1.9 mm wide, at middle plane and 1.3-4 mm wide, at tip barely cucullate round to abruptly acuminate and 0.15-0.3 mm wide, the veins 3-5, nectary cordate, 0.5-0.8 mm long and 0.55-1.2 mm wide, nectar often profuse; when pollen is first being shed the filaments surpassing the tepals, pale pink to red-purple, elongating to 5-7.5 mm long, elevated with the ovary on a column 0.3-1 mm above the perianth; unopened anthers saggitate, pink to peach-magenta; perianth in outline campanulate to urceolate, nodding when pollen is being shed; gynoecium when pollen is first being shed ovoid to plumply ellipsoid 4-4.5 mm long and 1.6-1.9 mm in diameter, white to red-purple; ovules 2-7 in each locule, placenta occupying middle of ovary suture; when pollen is first being shed styles, including stigmas, 1-1.2 mm long; usually only lower one-third of inflorescence producing fruit, the upper portion of the inflorescence often rotting and breaking off; mature capsules turbinate, 1-2 cm long and 1-2 cm in diameter, inflated, mounted on a column 1.8-2.2 mm above perianth, beaked by recurved styles, including stigmas, 0.5-1.5 mm long; seeds 1-3 (-4) in each of 2-3 locules; seeds irregularly plumply ellipsoid to rectangular or conic, 6-8.5 mm long and 4-5.2 mm in diameter, chestnut brown, deeply rugose to ruminant.

Pine-oak forests in the Sierra Madre de Oaxaca and in the southern portion of the Sierra Madre del Sur. Growing in moist, red

clay mixed with limestone. Elevation 2500-3200 m. Flowering May through July and fruiting August through September. Endemic to Puebla and Oaxaca (map 1).

A beautiful and striking species with red to red-green campanulate flowers, symmetrically arranged in a short, slightly to very condensed inflorescence. In each inflorescence, usually only the lower one-third to one-half produces the large, inflated turbinate fruits.

My experience collecting Schoenocaulon tenuifolium in the Sierra de Juaréz has been that populations are composed of many sterile plants and very few fertile ones, and that the fertile plants are often the oldest and largest individuals. In addition, ants appear to tend the fertile plants as well as to feed on the nectar and sometimes the very young capsules. Although ants and plants are sometimes co-adapted (albeit with few cases of strict myrmecophily), ants are usually marauders rather than pollinators. The red flowers that characterize S. tenuifolium do not occur elsewhere in the tribe, and the production of copious nectar is very rare in the genus. The nectar from this species has been analyzed by the late Irene Baker, and her results are presented in the chapter on Chemistry. Briefly, sucrose is the sugar found in the greatest proportion. Further studies are required to determine the nature and extent of this species' interaction with ants, as well as to learn what pollinates this lovely plant. Interestingly, tepals from plants of this species which grow to the north and west of the Sierra de Juaréz are not quite as brilliant red, but rather are red-green to magenta-green. Indeed,

plants from north of the Sierra de Juárez approach S. caricifolium var. oaxacense in the shape of their tepals, which are falciform in outline. This similarity in tepal shape suggests that S. tenuifolium may have been derived from S. caricifolium.

A few specimens show signs of having withstood burning. It seems likely that fires are rare in the region to which S. tenuifolium is endemic.

Additional Specimens Examined--

MEXICO

Puebla: Mpio Coxcatlán, 4 km al E de Pala, brecha a Zoquitlán (Tenorio et al. 14102, MEXU, UC).

Oaxaca: Cerro San Felipe, (Conzatti 688, GH; Pringle 5857, GH; Pringle 5851, MEXU; Pringle 6653, ENCB, F, GH, MEXU, MO, NY, UC, US; Pringle 10184, CAS, GH, F, MICH, MO, NY, UC, US, WIS; C. L. Smith 753, MO, NY, US); Dist. of Ixtlán, Mpio of Comaltepec, 0.5 km N of Rte Nacional 175 on road to Comaltepec (Frame et al. 272, MEXU, NY); Dist. of Ixtlán, Mpio of Comaltepec, "Agua Fría" 3 km N of turnoff (turnoff known as "La Machin") to Comaltepec from Rte Nacional 175 (Frame et al. 273, MEXU, NY; E. P. Portilla B-134, MEXU); 4.5 km NE of Cuajimoloyas, (Frame et al. 274, NY; M. Sousa 4610, MEXU); Cerro Verde S of Cuixtlahuaca (Frame et al. 320, MEXU, NY); a 6 km al N de Comaltepec, sobre la carretera, Dist. de Ixtlán de Juárez, (A. García M. et al. 638, MEXU); mountains southeast of Miahuatlán, 1895 (E. W. Nelson 2530a, US).

Figure 21. Schoenocaulon tenuifolium. Base of plant and inflorescence, x 0.8 (Frame et al. 273).



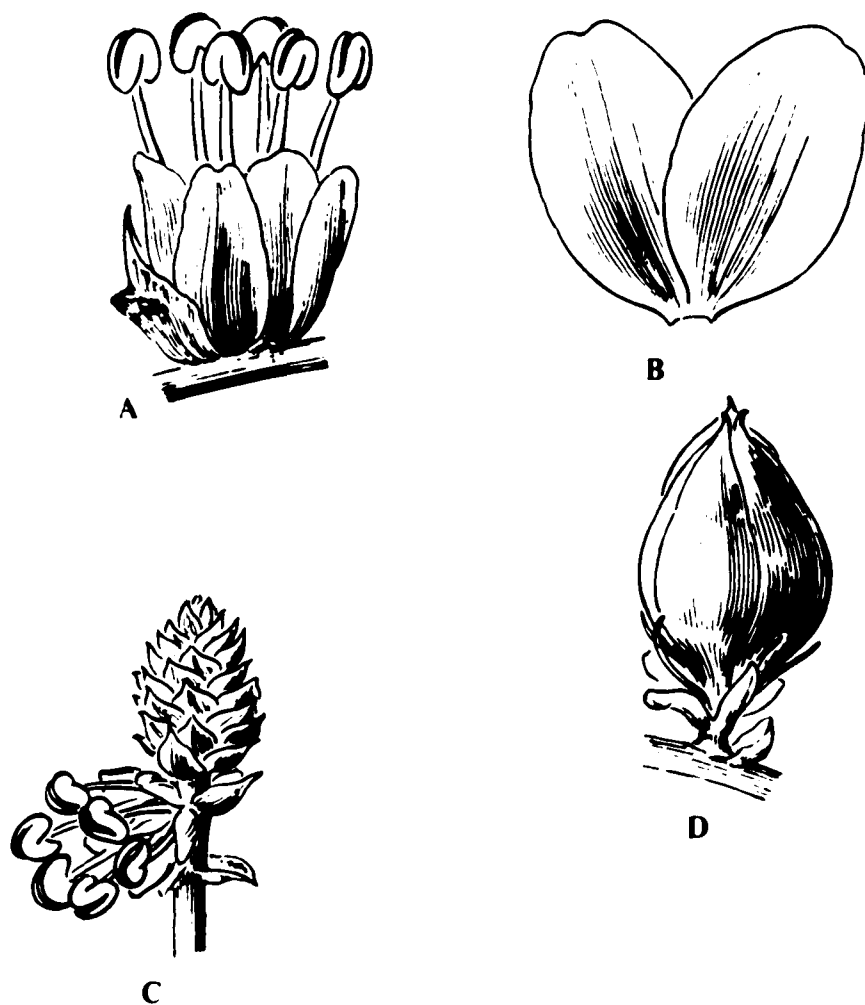


Figure 22. Schoenocaulon tenuifolium. A, mature flower shown with unopened anthers, x 6; B, two tepals, x 8; C, detail of termination of inflorescence, x 6; D, immature capsule, x 2 (A-C, Frame et al. 273; D, Frame et al. 272).

2. *Schoenocaulon officinale* (Schlecht. & Cham.) A. Gray ex Benth.,
Pl. Hartw. 29. 1840. **Type:** MEXICO. Veracruz: "In declivitate
orientale Andium Mexicanarum in Barranca de Tioselo prope la Hacienda
de la Laguna Mexico," (Schiede & Deppe 982, MO!, K!, isotypes).

Veratrum officinale Schlecht. & Cham., Linnaea 6: 45. 1831. Helonias
officinalis D. Don, Edinburgh New Philos. J. 13: 234. 1832. Asagraea
officinalis Lindl., Bot. Reg. 25: pl. 33. 1839. Sabadilla
officinarum Schlechtendal, Linnaea 18: 444. 1844. [nom. illeg.]

Veratrum luteum, sensu Sessé & Mociño: Pl. Nov. Hisp. 174. 1890;
Pl. Nov. Hisp. ed. 2. 162. 1893; Fl. Mex. 97. 1894; Fl. Mex. ed. 2.
89. 1894. [see note under heading of "Additional Specimens Examined"]
Figure 23.

Bulb ellipsoid to ovoid, 2-4.5 cm long and 1.7-4 cm in diameter,
enveloped underground by a tunic of papery to fibrous leaf-bases,
these forming a neck 4-19 cm long and 1-2 cm in diameter; leaves 6-13,
30-150 cm long, 6-15 mm wide, usually shorter than the raceme, green,
18-25-nerved, the nerves spaced 0.3-1.2 mm apart; scape 50-150 cm long
and 1.3-10 mm in diameter, the crowded 100-450-flowered raceme 23-60
cm long, nodding; flowers malodorous, mostly 8-ranked, when pollen is
first being shed pedicelled, the pedicels 0.5-2 mm long and 0.9-1.2 mm
in diameter, usually the uppermost one-third to one-half functionally
staminate and the uppermost 10-120 bracts empty or concealing
rudimentary flowers; bracts pentagonal, 2.5-3.3 mm long and 2-3.7 mm
wide, translucent, the veins 7-9, wine-colored, the margin erose;
pedicels of nearly mature to mature capsules 1.8-4 mm long and 0.8-1.2
mm in diameter, those of any vertical rank 10-18.5 mm apart; fruit in

weakly nodding inflorescence disposed parallel to axis; fruit in strongly nodding inflorescence usually disposed at right angles to the ground, the pedicels variously oriented; tepals when pollen is first being shed 3.8-4.7 mm long, ligulate, dilated at base near nectary, cream-colored, opaque to nearly translucent, fleshy, at base 0.4-0.8 mm wide, sometimes connate through 0.5 mm, in distal two-thirds 0.5-1 mm wide, the tip round to acuminate, cucullate, the veins 3, sometimes convergent short of tip, otherwise the lateral ones expiring short of tip, the central one nearly reaching tip; nectaries well-developed, round to oval, 0.6-0.8 mm long and 0.7-1.5 mm wide; filaments when pollen is first being shed surpassing the tepals, outer whorl maturing first, white, continuing to elongate with the opened anthers to 6 mm, the anthers then shed; unopened anthers sagittate, yellow to yellow-green; gynoecium when pollen is first being shed ellipsoid, 3.3-3.8 mm long, 1.2-1.7 mm in diameter, white; ovules 6-12 in each locule, placenta occupying lower two-thirds to three-quarters of suture; styles, including stigmas, 0.7-1 mm long; capsules ellipsoid to ovoid, 8.5-17.5 mm long, 3.2-7 mm in diameter, beaked by styles, including stigmas, 1-1.5 mm long; seeds 1-4 (-5) in each locule, ellipsoid to conic or falciform, 5-7.5 (-9.5) mm long, 1.3-2.2 mm in diameter, golden-brown to chestnut, reticulate-foveate to striate, with thin membranous appendages formed at each end at contact points between seeds, ultimate seed strongly beaked.

Sunny places in savannas, oak forest, pine-oak forest, or rocky hills, from central Mexico through Central America to northern South America, 100-2000 m, flowering June through September. This is one of

the few species of Schoenocaulon that may be found growing in disturbed habitats (map 2).

The inflorescence of this species is late to expand, and it is only after dehiscence of the anthers that there is room for the perianth to open completely thereby exposing the relatively highly-specialized nectaries, at which time the tepals are sometimes reflexed. Local races may produce double flowers having 7-12 tepals, 6-12 stamens and 3-9 carpels, which suggests that this species was cultivated widely in the past. The only known report of insect visitors to S. officinale comes from Kruse's collection from Guerrero (Kruse 724) in which he mentions that the flowers are aromatic and visited by hymenoptera and lepidoptera. The nectaries of S. officinale are unlike those of all other Schoenocaulon species in that they are formed by an elaboration of tissue and appear as "pads". It may be that a slight pressure upon these pads releases the nectar. In flowers which show signs of frequent feeding by insects the pads are dug out, leaving a deep pit.

In 1891, Palmer collected fruiting stalks of this species in a market place in Colima, and assigned the number 1410 to them. Rose mentions this number as perhaps representing a species of Hechtia (J. N. Rose, Contr. U.S. Nat. Herb., 1: 359. 1895). Schoenocaulon officinale has not been found wild in Nueva Galicia, and Palmer's sample may have been imported from elsewhere or cultivated locally. Similarly, Standley bought some inflorescences in Tegucigalpa from a market woman who presumably collected them somewhere near Santa Lucía (see chapters on chemistry and ethnobotany).

Additional Specimens Examined--

MEXICO

Colima: Colima (Palmer 1410 in 1891, GH, US).

Michoacán: Zitácuaro-Piedra de Cal (Hinton et al. 13226, GH, MICH, MO, NY, US).

Guerrero: Hwy 95, ca 6.4 km by road N of El Rincón (W. R. Anderson 12920, MICH, UC); Distrito Mina, Santa Teresa (Hinton et al. 9397, NY, UC, US); Distrito Mina, Puerto del Clarín Cayunche (Hinton et al. 9506, NY, US); Distrito Mina, Calavera-Puerto (Hinton et al. 9539, GH, NY, US); Rincón Viejo, just SW of Agua de Obispo (Kruse 724, ENCB).

México: Chorrera, Disto Temascaltepec (G. B. Hinton 2039, F, US); Telpinela, Disto. Temascaltepec (G. B. Hinton 2420, CAS).

Morelos: Xochicalco (E. & C. Seler 5379 (296), GH).

Oaxaca: Santa Efigenia (E. W. Nelson 2847, US; E. W. Nelson 2849, F); San Benito, near Apango (B. Reko 3475, US) [note, I have been unable to locate either town in Oaxaca, although there is an Apango, Guerrero]; Mpio San Pedro Tapanatepec, 17.1 km al NE de Rodolfo Figueroa, camino a Díaz Ordáz, entrando por Rizo de Oro (R. Torres & C. Martínez 10609, MEXU, UC).

Veracruz: Orizaba (Botteri 1186, GH, US; Bourgeau 2981, GH, US; F. Miranda 747, MEXU; June 1897, C. Mohr & Botteri s. n., US; F. Müller 222, GH, NY); Consoquitla (Liebmann 14625, F); Mirador (Liebmann 14627, F; Liebmann 14628, F, GH, UC, US; H. Rose 750, US); Zacuapan, Fortín (Purpus 2023, F, GH, MO, NY, UC, US); 6 km al SE de San Pedro Soteapan, vertiente sur de la Sierra de Santa Marta, región

de Los Tuxtlas (M. Sousa 3242, MEXU); slopes of Cerro de Escamela, N of the town of Orizaba on road to Ojo de Agua (R. Weaver et al. 1767, MICH).

Chiapas: Mpio of Tenejapa, trail from Habenal to Tsahal Kesh in the paraje of Mahben Chauk (Breedlove 6394, DS, ENCB, F, MICH); Mpio of Ixtapa, along Mex. Hyw 190 in the Zinacantán paraje of Muctajoc (Breedlove 11850, DS; Frame & Geddes 267, MEXU, NY; R. Laughlin 1155, DS; R. Laughlin 1265, DS, MICH, NY; R. Laughlin 1548, DS, F; R. Laughlin 1842, DS, WIS); Mpio of Totolapa, 6-8 km W of Teopisca on the side of Cerro Chenek'ultik (Breedlove 27070, DS, MO); Mpio of Las Margaritas, 8 km E of Las Margaritas on road to La Soledad (Breedlove 37895, CAS); Mpio of Villa Corzo, ridge above Colonia Vincente Guerrero on road to Finca Cuxtepec (Breedlove & Strother 46565, CAS); Mpio of Tuxtla Gutiérrez, slope at El Sumidero, 20 km N of Tuxtla Gutiérrez (O. Clarke 233, DS, RSA); Camino al Cañón Sumidero (Gómez-Pompa 2581, DS); Mpio Chiapa de Corzo, 40 km al W de San Cristóbal Las Casas, camino a Tuxtla Gutiérrez (E. Martínez 6806, MEXU); Siltepec (Matuda 1600, DS, F, MICH, NY, US); Mpio of Tenejapa, along the river Tanate' in the barrio of Habenal, paraje of Mahbenchauk (Ton 335, DS); Mpio Amatenango del Valle, along the "Chenek' Ha" creek near Amatenango (Ton 2694, DS).

Without definite locality: "Plantae mexicanae Liebmann". (Liebmann 14629, F); "Mexico. (Hooker dupl. 1839)"--note appears to be in Asa Gray's handwriting, collector unknown.

Before me I have one specimen (J. J. Linden 56, MICH), which, according to W. Botting Hemsley in *Biologia Centrali-Americana* (3:

383), comes from "Zimapan". It is highly improbable that it was collected in Zimapán, Hidalgo, although it is likely to have come from Mexico.

I have a specimen from the Field Museum [Sessé & Mociño 23-I 1994 3813] which according to the account of Veratrum luteum [L.], sensu Sessé & Mociño grows "in temperate regions, Mazatlán [Guerrero] and elsewhere in New Spain" (transl. and pers. comm., R. McVaugh). As Sessé & Mociño did not use collection-numbers as we know them the following is a brief explanation of the significance of the numbers on the label (this information was kindly provided by R. McVaugh).

"23-I" refers to the Linnean class and order to which Sessé & Mociño assigned the plant.

"1994" is the number assigned to that species, although it does not distinguish any particular specimen.

"3813" is the number assigned to the item by workers in Madrid in 1935 or 1936 before the specimens were shipped to Chicago for identification.

This particular specimen does not appear to have been photographed at F as no Chicago negative number (a five-digit number) is present.

GUATEMALA

Huehuetenango: inter Uaxackanal [Uaxacanal] et Quen Santo (E. & C. Seler 3220, GH); prope Chaquial (E. & C. Seler 3273, GH, US); between Democracia and canyon of Chamushú (Steyermark 51215, F); between Nentón and Las Palmas, via Yalisjao, Rincón Chiquite, Chaquial, Guaxacaná, in Sierra de los Cuchumatanes (Steyermark 51615,

F).

Chimaltenango: Alameda, Chimaltenango (J. R. Johnston 961, F, NY).

Guatemala: "Dept. Guatemala" (I. Aguilar 128, F); 10 km S of San Raimundo (Standley 62922, F).

Santa Rosa: Rio de Los Esclavos (Heyde & Lux 3874, GH, NY, US).

Jutiapa: Lago Retana, between Ovejero and Progreso (Steyermark 32025, F).

Chiquimula: Montaña Castilla, vicinity of Montaña Cebollas, along Rio Lucía Saso, 3 miles SE of Quezaltepeque (Steyermark 31227, F).

Zacapa: lower slopes of Sierra de las Minas, along trail above Río Hondo (Steyermark 29548, F).

Without definite locality: "In praeruptis Guatemala" (Hartweg 627, NY).

• HONDURAS

Copán: Piña creek, vicinity of el Pinal (A. Molina et al. 31133, F).

Comayagua: 10 km east of Siguatepeque (Hazlett 2134, MO); about 6 km W of Siguatepeque (Yuncker et al. 6385, F, GH, MO).

Morazán: entre Las Mesas y Guayabillas, 5 km empalme carretera Danlí-Yuscarán (A. Molina 13161, F, NY, US); Santa Inés (Juvenal Rodriguez 472, F).

Tegucigalapa: Tegucigalapa, "Bought from market woman from Santa Lucía" (Standley 26707, F, MO, US).

El Paraíso: km 73 entre El Ojo de Agua y Río California (A.

Molina 14480, F); Sierra de la Villa Santa, 5 km W of Jacaleapa (L. Williams & A. Molina 10490, F, GH, MO); Sierra California (L. Williams 18575, F).

EL SALVADOR

Santa Ana: Cerro de San Jacinto (S. Calderón 1060, GH, MO, NY, US).

San Salvador: Vicinity of San Salvador (C. Renson 167, NY, US).

COSTA RICA

Guanacaste: between lumber mill and Esso station, ca. 1 km south of La Cruz (A. Weston 1853, UC).

Alajuela: Nuestro Amo (Otón Jiménez 637, US).

VENEZUELA

Trujillo: Carretera Valera-Boconó, cercanías de Boconó, ca. 6-8 km E of the city (M. López-Figueiras & J. Dugarte 29408, US).

Aragua: Along Hwy no. 4 between La Victoria and Colonia Tovar; 17 km S of the center of Colonia Tovar (Croat 54422, MO); "Prope coloniam Tovar" (Fendler 1506, GH, MO); Disto Ricaurte, 12-18 km al norte de La Victoria, hacia la Colonia Tovar (Steyermark et al. 127732, MO).

Miranda: hills above los Teques (Pittier 11611, NY, US); Camino El Naranjal, Cortada del Guayabo (Tillett 839-55, NY); Los Chorros (Ll. Williams 12398, F, MICH).

Distrito Federal: hills above Caracas (H. Brett s. n. cf. Rose et al. 21887, US; Brother Elias 71, F; A. Ernst s. n., US; R. Labbiente 71, US; A. Lawrance 888, NY; Pittier 7352, GH, US; Pittier 9556, GH, US; Rose et al. 21887, NY, US; D. Williams no. 1, 2, & 3,

WIS; Ll. Williams 13604, F).

Without definite locality: "Eggers Rejse til Venezuela 1891"
(Eggers 13361, F, US).

PERU

Ayachucho: San Miguel, Urubamba Valley (Cook & Gilbert 1013,
US).

Cuzco: Santa Ana (Cook & Gilbert 1538, US); Prov. La Convención,
Valle de Santa Ana above Quillabamba (Plowman & E. Davis 4782, GH);
Prov. La Convención, Potrero (C. Vargas 1844, GH; C. Vargas 23456,
MO).

Figure 23. Schoenocaulon officinale (Asagraea officinalis). Copy of tabula 33 in Lindley (1839).

33



3. *Schoenocaulon pellucidum* Frame in McVaugh, Flora Novo-Galiciana
 15: 272-274. 1989. **Type:** MEXICO. Nayarit: "along road from Hwy
 15 to Santa Cruz [w of Tepic], about 9.9 mi W of Hwy 15," (Warren
Douglas Stevens 1489, MICH!, the holotype; ENCB! isotype).

Figure 24.

Bulb ovoid to ellipsoid, 2.5-4 cm long and 2.5-3 cm in diameter, enveloped underground by layers of brown papery leaf-bases, these forming a neck 3-7 cm long and 1-2 cm in diameter; leaves 6-10, usually soft and pliant, 30-70 (-100) cm long, 4-14 mm wide, green, 16-25-nerved, the nerves spaced 0.3-0.6 mm apart; scape 95-155 cm long, 2.2-8 mm in diameter, mostly longer than the leaves, the condensed raceme (6-) 8-23 cm long, (50-) 80-225-flowered; flowers 5-8-ranked, when pollen is first being shed pedicelled, the pedicels 0.8-1.7 mm long and 0.5-0.7 mm in diameter, often one-third to one-half of the uppermost flowers functionally staminate; uppermost 25-80 bracts empty or concealing rudimentary flowers, compressed into a narrowly to plumply campanulate crown; bracts narrowly to broadly pentagonal, 2-2.7 mm long, 1.2-2.3 mm wide, translucent, 4-6-nerved, the margin erose; pedicels of nearly mature to mature capsules 2.5-5 mm long and 1-1.2 mm in diameter, those of any vertical rank 3.2-13 mm apart, those of immature and staminate flowers perpendicular to axis and those of fruits ascending at 10-45° from stem or sometimes sharply curving upwards disposing mature fruits parallel to scape; tepals 2.8-5 mm long, variable from linear without auricles to distinctly auriculate, translucent, petaloid to slightly fleshy, cream-colored to pale green, 3-5-nerved, at base deeply 3-nerved with shiny

nectariferous tissue, canaliculate adaxially and 0.4-1 mm wide, there sometimes connate through 0.3 mm, at middle plane to weakly canaliculate 0.4-0.9, at tip acute to apiculate, cucullate and 0.4-0.7 mm wide; filaments equalling or surpassing tepals when pollen is first being shed, white, continuing to elongate until 5-7 mm long, the anthers then shed; unopened anthers cordiform, yellow; gynoecium ampulliform, when pollen is being shed if functional 2-3.5 mm long and 1.3-1.8 mm in diameter, if non-functional slightly collapsed, 1.2-1.7 mm long and 1-1.2 mm in diameter, white, the ovules 3-6 in each locule, placenta inserted on lower half of ovary suture; when pollen is first being shed styles, including stigmas, 0.5-0.9 mm long; capsules narrowly ovoid to ovoid, 9-15 mm long and 4-6 mm in diameter, opening one-third to one-half lengthwise along septum, the sides becoming parallel, the persistent styles, including stigmas, 1-3 mm long; seeds 1-3 in each locule, golden to chestnut brown, irregularly linear-ellipsoid, 5-7 mm long and 1.5-2 mm in diameter, undulate to rugose-reticulate, with thin membranous appendages formed at each end at contact points between seeds.

Locally abundant on ungrazed steep rocky hills under oaks or on grassy mountainsides of the Pacific slope in the states of Nayarit, Jalisco, and Michoacán (map 3). Elevation 500-1350 m. Flowering August through September and fruiting late September through November.

This species has been confused with Schoenocaulon officinale, which however differs in having clearly differentiated floral nectaries. Schoenocaulon pellucidum bears some similarity to S. ghiesbreghtii Greenm., particularly with regard to the papery bulb

scales and often petaloid tepals. It probably represents a vicariat of that species in the mountains of the Pacific slope. Schoenocaulon ghiesbreghtii is distributed through the Gulf coastal plain from Texas to the Yucatán Peninsula and Chiapas, and differs in having short-ovate, not long-linear tepals with erose, not entire, margins, and stamens not elongating until almost twice as long as the tepals. Some features of plants growing in the Cerro de Carboneras approach those of Schoenocaulon mertonii. The material I have from there lacks the bulb (and consequently papery bulb scales) which readily distinguish S. pellucidum. Nonetheless, although the leaves tend to be somewhat narrower, the tepals a bit more leathery, and the raceme somewhat looser, these plants still more closely resemble S. pellucidum and are here included. Schoenocaulon pellucidum is remarkable for its shallowly buried bulb with papery bulb scales, its wide, pliant, many-nerved leaves, its long scape which is at least 3 times the length of the inflorescence, its usually very condensed raceme, and its cream-colored to pale green translucent tepals with nectariferous tissue discernable as shiny epidermal cells.

Most of the species of the Pacific coast and adjacent mountains have an exceptionally long scape, an otherwise relatively rare character. This shared character suggests a common origin of these species or alternatively represents the introduction of a dominant genetic feature into several not necessarily originally closely related evolutionary lines. Whatever the case, there can be no doubt that S. jaliscense, S. megarrhizum, S. mertonii, S. pellucidum, and S. tigrense are closely related.

Additional Specimens Examined--

MEXICO

Nayarit: along Hwy 28 (route 66 on some maps), between Tepic and Jalcacatlán [Jalcocotán] (Croat 45246, MO); ca. 12 miles W of Tepic, 6.5 miles E of Jalcocotán (McVaugh 18804, MICH, NY); 4-5 miles north of Compostela (McVaugh 19344, MICH, NY).

Jalisco: entre El Tuito y Pto. Vallarta, a 20 km de Pto. Vallarta (Delgado, Hernández & Trejo 160, MEXU, MICH); barrancas W of La Quemada (Pennell 19923, US); 2 mi NW of Tequila (McVaugh 18615, MICH); mountains 3 miles S of La Huerta, road to Barra de Navidad (McVaugh 19819, MICH, NY).

Michoacán: west-facing slopes of Cerro de Carboneras above the Río Cupatitzio, ca 22 km S of Uruapan (King & Soderstrom 4915, MICH, NY, US).

Figure 24. Schoenocaulon pellucidum. Base of plant, x 0.5; seed, x 5; capsules after and before opening, x 3.5 (all from Delgado et al. 160); fruiting spike, x 0.5 (McVaugh 18804); flowering spike, x 0.5; a, immature flower, and its gynoecium with one stamen, x 5; b, mature flower after anthers have abscised, x 5 (all from McVaugh 18615); c, young capsule, x 5 (McVaugh 19344). Illustration originally published in Flora Novo-Galiciana, vol. 15, R. McVaugh (1989), and here used with the kind permission of Dr. McVaugh and the University of Michigan Herbarium.



4. *Schoenocaulon ghiesbreghtii* Greenman, Proc. Amer. Acad. 43: 20.

1907. **Type:** MEXICO. Chiapas: "Chiapas, etc.:" (Ghiesbreght 672, GH!, the holotype; MO!, NY!, isotypes).

Schoenocaulon drummondii A. Gray ex Torrey, U.S. & Mex. Bound.

Surv. 2: 222. 1859. [nom. illeg.] **Type:** UNITED STATES. Texas (T. Drummond 284, Coll. III, GH!, NY!, TCD!, isotypes). Sabadilla drummondii Kuntze, Rev. Gen. Pl. 2: 713. 1891.

Schoenocaulon yucatanense Brinker, Ann. Missouri Bot. Gard. 29:

307. 1942. **Type:** MEXICO. Yucatán: "Uxmal, on base of large pyramid" (Steere 2093, NY!, the holotype; MICH!, isotypes).

Figure 25 & 26.

Bulb narrowly ovoid to spherical, 2.5-6 cm long and 2-5.5 cm in diameter, the rhizome short and generally appressed to the side of the bulb, enveloped underground by layers of brown papery leafbases, these forming a neck 2-10 (-19) cm long and 0.8-2.5 cm in diameter of papery brown to moderately coarse dark brown fibers; leaves 6-11, 20-75 cm long and 2.8-11 mm wide, usually shorter than or equalling the raceme, green, 10-16-nerved, the nerves spaced 0.1-1.2 mm apart; scape 21-93 cm long, 1.2-8 mm in diameter, straw-colored, purple at base and often towards and within inflorescence, the condensed 45-180(-300, if cultivated)-flowered raceme 5-23 cm long; flowers mostly 4- or 8-ranked, when pollen is first being shed sessile to pedicelled, when present the pedicels no more than 1 mm long and 1.2 mm in diameter, the uppermost 3-40 flowers often functionally staminate, the uppermost 20-85 bracts empty or concealing rudimentary flowers forming a plump to narrow dome crowning the raceme; bracts irregularly pentagonal to

broadly obovate, 1.2-2.8 mm long and 1.2-3.3 mm wide, membranous, with 4-6 wine-colored veins, margin crenulate to erose; pedicels of nearly mature to mature capsules ascending at 35-45° from stem or curving upwards disposing fruit parallel to scape, 1-3 mm long, 0.8-1.5 mm in diameter, those of any vertical rank 8-14.5 mm apart; tepals when pollen is first being shed 1.5-4.7 mm long, linear, ovate, obovate or triangular, at base canaliculate adaxially and 0.3-0.7 mm wide, at middle plane to convex or canaliculate adaxially and 0.5-2.2 mm wide, at tip cucullate, acute to blunt and 0.1-0.4 mm wide, 3-5-veined, center of blade green to green-pink or green-purple, opaque, slightly-fleshy, margin of blade crenulate to slightly dentate, translucent, hyaline to pinkish; nectary usually well-developed, appearing as a moderately deep to deep semi-lunate depression at base of tepals; filaments when pollen is first being shed at least nearly twice the length of the tepals, white, often dilated above and ascending at 40-80° from stem, sometimes continuing to elongate to about 2.5 times the length of the tepals and turning pink-purple; the unopened anthers narrowly sagittate, greenish yellow to peach-purple; gynoecium when pollen is first being shed narrowly ampulliform 3.7-5.4 mm long and 1.2-1.7 mm in diameter, white, becoming streaked with pink upon fertilization; ovules 4-9 in each locule, placenta occupying lower one-half of suture; when pollen is first being shed styles including stigmas 0.6-1.1 mm long; young capsule elevated with the filaments on a column 0.2-1 mm long above the perianth, or rarely this lacking; capsules ellipsoid to ovoid or nearly campanulate, 8.5-13.5 mm long, 4-7 mm in diameter, often with pink-purple streaks or

entirely purple, beaked by styles including stigmas 0.7-1.5 mm long; seeds 1-4 in each of 2-3 locules, plumply ellipsoid, conic, semi-lunate, or rhomboid, 3-5 mm long, 1.5-2 mm in diameter, chesnut to dark brown, striate to striate-rugose, with a light brown ridge running the length of the concave face and crowning the distal tip. Please note, the dimensions of plants cultivated at the Texas Agricultural Experimental Substations and in Wisconsin, have not been here included, and those plants are larger in almost all details.

Locally abundant in sandy to moderately rich soils from sea level to 2,700 m. In the United States, this species grows almost exclusively on the Reyosa gravel formation of the Texas gulf prairie. In Mexico its pattern of distribution coincides with the eastern portions of Rzedowski's "bosque tropical caducifolio" (Rzedowski, 1983). Occasionally growing along streams in low elevations, at high elevations this species is restricted to riparian habitats (map 4). In Texas flowering August through October and fruiting October through December; in Mexico flowering May through August and fruiting July through September.

The familiar name for this taxon is S. drummondii, and Asa Gray is commonly considered the authority, based upon his published letter in Bot. Beechey Voy., p. 388, (1840); however, no description was provided therein, hence the name was not validly published. Torrey, believing that Asa Gray had validly published the name, listed S. drummondii in the Botany of the Boundary (U.S. & Mex. Bound. Surv. 2: 222. 1859.) and cited Gray, but at the same time placed S. texanum Scheele, an earlier validly published name for a different taxon, into

synonymy under S. drummondii, thereby making the name S. drummondii superfluous and hence illegitimate. Nonetheless, it is quite clear that Torrey considered T. Drummond 284, Coll. III the type for the species. Brinker in his Monograph of Schoenocaulon (1942) mentions that among the Holographic notes of Dr. A. Gray is a reference to reducing S. texanum to synonymy under S. drummondii, although apparently Gray never effected this in a formal publication. In 1916, Pennell sorted out the differences between S. texanum and what had generally been called S. drummondii, although the latter name remains illegitimate. Greenman described S. ghiesbreghtii from material collected by Ghiesbreght in Chiapas. I consider S. ghiesbreghtii conspecific with S. drummondii A. Gray ex Torrey and S. yucatanense Brinker.

Much of the confusion surrounding the circumscription of Schoenocaulon species may be attributed to the following three facts: that only one species S. officinale, was ever illustrated before 1989; that most species descriptions have been cursory; and that owing to rarity in nature there are relatively few specimens. The key characters of S. ghiesbreghtii are bicolored, either green-cream or pink-green tepals with crenate margins and filaments nearly thrice the length of the tepals. Another characteristic of this species is the serpentine form of the inflorescence when in blossom. This form is produced because the filaments expand very rapidly, whereas elongation of the inflorescence is comparatively slow. In this way, the weight along the inflorescence is unequally distributed and leads the maturing inflorescence to nod or appear serpentine. Recent

collections by Vaughan et al. and Breedlove, have provided specimens that link the lowland to the upland forms of this species. Brinker had a good conception of S. drummondii in the north but did not comprehend its southern relatives. This is not surprising in view of the fact that the material of S. ghiesbreghtii available to him consisted of three very old specimens in rather poor condition, and his newly described taxon S. yucatanense was based on a single collection. With the material available to me, as well as field experience, I confidently unite these three taxa.

The collections of S. ghiesbreghtii from Chiapas are particularly robust, which may be related to the rich mountain soils and abundance of water, or to past cultivation, or both. I have observed specimens of cultivated S. ghiesbreghtii from Texas which attain similar size and stature as those from Chiapas, supporting the view that nutrient-poor sandy soils and variable precipitation place limits upon the dimensions of the species. As part of her Huastec Ethnobotany Project, Janis Alcorn made specimens of some plants that were originally identified as Schoenocaulon officinale. Although the material is very young, the NY specimen of Alcorn 2153 proves to be S. ghiesbreghtii. The label information states that the common Huastec name for this plant is "cebadilla" (the common Spanish name, see chapter on Ethnobotany) and that it is recognized as a medicinal plant although the Huastec Indians do not intentionally cultivate or otherwise protect it. That today at least some indigenous people still recognize this species as a medicinal plant suggests the interesting proposal that the now upland Chiapan form of this species

was originally a hardy variety of the lowland one which was deliberately carried to, and and cultivated in, the mountains of Chiapas by the Indians.

At Uxmal in the Yucatán, I observed small bees collecting pollen from the flowers, whereas further north in Veracruz I noted skippers (Hesperioidae) feeding on nectar produced at the base of the tepals. The nectariferous tissue is obscure on most dried pressed specimens, but rarely it may be discerned as a dark, glistening region at the base of the tepals. Boiling the flowers for too long often obliterates most signs of the nectary. Minor differences in such characters as flower shape, size, color, presence or absence of a column raising the sexual apparatus above the perianth, and amount and type of nectar produced may be related to local pollinator pressures, a proposition that deserves further study.

The plants from the Chiapan highlands are distinct enough to warrant an infraspecific rank. The remaining populations from near the gulf coast of Texas and Mexico, however, do not lend themselves easily to division although they most probably have attained a comparable level of genetic isolation and diversification. For this reason, I have chosen not to recognize any infraspecific taxa at this time. In the future, after close study of the populations of this intriguing species, a reasonable treatment for their segregation into infraspecific categories may be devised.

Additional Specimens Examined--

UNITED STATES

Texas: Kleberg Co., Kingsville (E. Bogusch S-86, US); San

Patricio Co., 5.5 miles southeast of Mathis (Correll 20418, MO, NY, UC; Rose & Russell 24160, NY, US); San Patricio Co., about 4 miles NW of Sinton (C. M. Rogers 6646, RSA); Gonzales Co., 2 miles S of Belmont (Correll 20467, RSA); Gonzales Co., Mills Creek (28 May 1942, H. B. Parks, GH); Duval Co., 25.6 miles NW of San Diego (Cory 16146, GH); Bee Co., $\frac{1}{2}$ mile S of Tuleta (Cory 20644, GH); Bee Co., Beeville (M. E. Jones [29080?], POM, MO, UC); Edwards Co., garden of Texas Agricultural Experimental Substation No. 14. "Cultivated. Bulb from Blanco County." (Cory 40215, GH); Aransas Co., Aransas Refuge (Cory 45821, GH); Jim Wells Co., Romarsid Ranch (B. & R. Freeborn 159, NY); De Witt Co., junction of routes 111 & 183 (H. S. Gentry & A. Barclay 18549, US); De Witt Co., roadside near Yorktown (6 October 1851, A. Schott, NY); Guadalupe Co., Seguin (Groth 202, CAS, F, GH, NY, US); Wilson Co., Sutherland Springs (Palmer 1322, GH, NY, US); Bexar Co., cultivated at San Antonio (29 October 1941, H. B. Parks, WIS); Colorado Co., 3 miles E of Alleyton (Pennell 5557, NY); Bexar Co., San Antonio (October 1837, Riddell, US); Goliad Co., open prairie near Goliad (Rev. C. Williams 91, F, MO); without definite locality [but see below] (1 October 1935, H. B. Parks, GH); without definite locality (Riddell 52, NY); without definite locality (Schlottmann s. n., US).

MEXICO

San Luis Potosí: Mpio de San Antonio, Tanjasnec (Alcorn 2153, NY); Tamazunchale, Cerro de S. Francisco (P. Maury 6257, GH); San Dieguito (Palmer 119, F, MO, NY, US).

Veracruz: Mpio Apazapan, along road from Baños de Carrizal to

Emiliano Zapata [=Carrizal], 2-6 km SE of Emiliano Zapata (Hansen & Nee 7472, MO, F; Frame & Tenorio 386, K, MEXU, NY, UC, etc.).

Yucatán: at base and on top of Temple of the Magicians, ruins at Uxmal (C. Bunting 4, WIS; Frame & Geddes 265, K, MEXU, MICH, NY, UC etc.).

Quintana Roo: Coba (Lundell et al. 7735, GH, MICH, US).

Chiapas: hillside facing south along the Pan American Hwy to Comitán, just outside of San Cristóbal (Alava 1331, DS); Mpio of Tenejapa, W of Tenejapa Center along trail to Paraíso (Breedlove 6842, DS, ENCB; Breedlove 6844, DS, ENCB); Mpio of Tenejapa, slope along the river of Chik Ha', barrio of Yashanal, paraje of Matsab (Breedlove 11100, DS); Mpio of Venustiano Carranza, 3 miles S of Aguacatenango along rd to Pinola Las Rosas (Breedlove 11221, DS); Mpio of Jitotol, steep slopes adjacent to large double waterfall, 6-8 km W of Jitotol (Breedlove 26388, DS, MO); Mpio of Jitotol, 6 miles N of Jitotol (Thorne & Lathrop 41370, DS); Mpio of San Andrés Larrainzar, near summit of Chuchil Ton, NE of Bochil (Breedlove 26803, DS, MO); Mpio of San Cristóbal Las Casas, forest on road to San Lucas Zapotal, 2-4 km from Mex. Hwy 190 (Breedlove 39561, DS); Mpio of Zinacantán, steep slope below Paraje Navenchauk (Breedlove 51844, CAS); Mpio of Zinacantán, slope in the paraje Sek'emtik (R. Laughlin 1257, DS); Fenia [Rancho Fénix--see Sousa S., 1969] (Purpus 405, US); 30 miles N of Palenque along MEX 186 [label says "Campeche", but if the mileage is correct then it must fall within the borders of the state of Chiapas] (J. Vaughan et al. 237, MO); without definite locality "La Sabadilla de tierra fria. Chiapas. 7000' "(C. H. Berendt s. n., GH).

In a report filed by H. B. Parks, he mentions that his 1934-37 collections were sine numero and came from between Corpus Christi and San Antonio. This "Report on Experiments with Sabadilla in Texas in 1942. Agricultural Research Laboratory San Antonio", formed part of a larger document. A copy of the full report was sent to Dr. Noble Clark at the Agricultural Experimental Station, University of Wisconsin, Madison, where it is now mounted on a herbarium sheet at WIS. The experimental transplantings of S. ghiesbreghtii by workers at the Texas Agricultural Experiment Stations have added to the confusion surrounding its natural distribution.

Figure 25. Schoenocaulon ghiesbreghtii. Plant in flower, x 0.8
(Frame & Geddes 265).



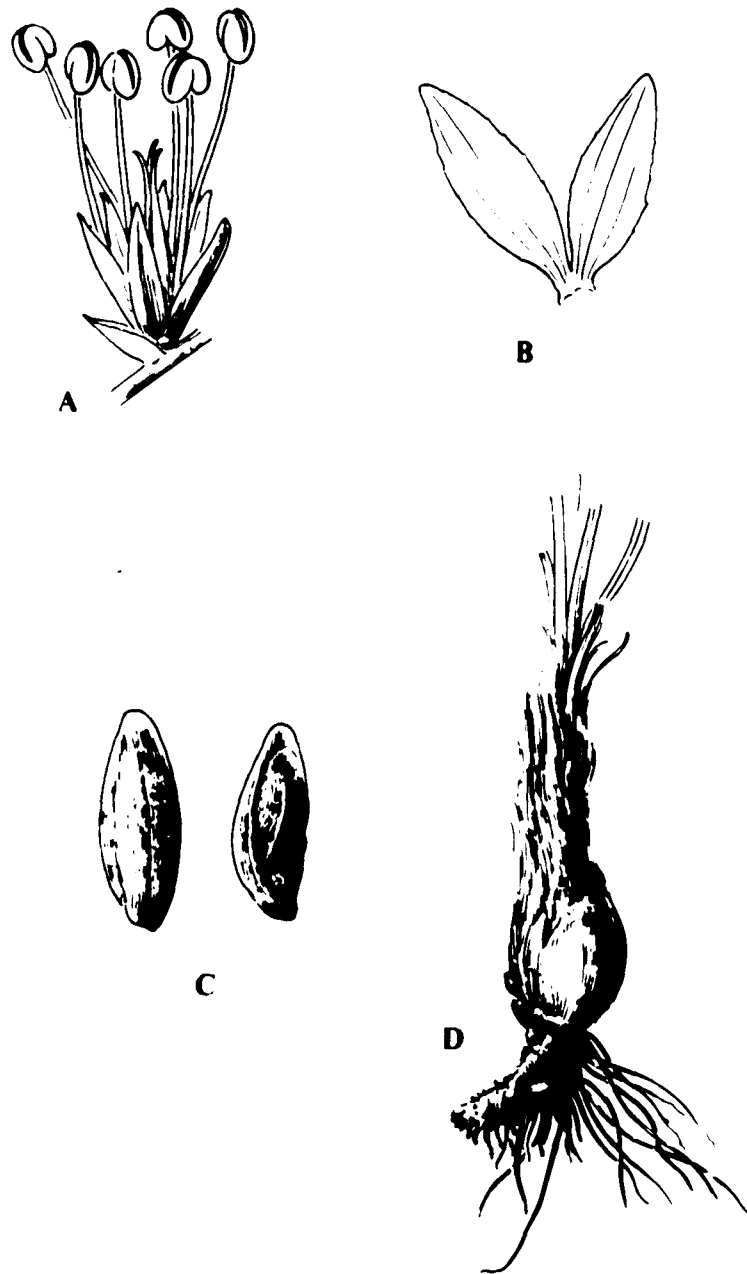


Figure 26. *Schoenocaulon ghiesbreghtii*. A, mature flower shown with unopened anthers, x 8; B, two tepals, x 12; C, seeds, x 6.5; D, detail of bulb-rhizome, x 0.8 (all from Frame & Geddes 265).

5. *Schoenocaulon tigrense* Frame in McVaugh, Flora Novo-Galiciana 15: 274-275. 1989. **Type:** MEXICO. Jalisco: Sierra del Tigre, "3 mi" S of Mazamitla (McVaugh 13041, MICH!, the holotype; NY!, isotype).

Shallowly buried bulb ellipsoid to ovoid, 1.8-3 cm long and 8-16 mm in diameter, enveloped underground by layers of dark brown papery leaf-bases, these forming a neck 3-4.5 cm long and 5-10 mm in diameter composed of fine to coarse brown fibers; leaves 5-7, 20-50 cm long, 1.5-3.5 mm wide, usually shorter than the scape, green, 6-9-nerved, the nerves spaced 0.2-0.3 mm apart; scape 40-80 cm long, 2-3 mm in diameter, when dry the vascular tissue visible as dark lines, the condensed 20-40-flowered raceme 5.5-11 cm long; flowers 5-ranked, not seen at anthesis, the uppermost 5-10 functionally staminate and the uppermost 5-20 bracts empty or concealing rudimentary flowers forming a moderately loose to slightly compact dome; bracts broadly ovate to broadly pentagonal, 2.2-2.5 mm long, 3.2-3.6 mm wide, translucent, the veins wine-colored, 4-5, the margin erose; pedicels of nearly mature to mature capsules ascending at 50-70° from stem, disposing fruits not quite parallel to scape, 0.5-2.5 mm long, 0.7-1.1 mm in diameter, those of any vertical rank 16-18 mm apart; tepals 2.5-3.5 mm long, oblanceolate to narrowly obovate, cream-colored to yellow-green and pale green, translucent, flacid, petaloid in texture, at base connate through 0.2-0.25 mm, canaliculate adaxially and 0.4-0.6 mm wide, at middle plane and 1-1.3 mm wide, at tip cucullate, acuminate to apiculate and 1.2-1.4 mm wide, the veins 3-4, sometimes obscure, the lateral ones expiring short of tip, the central one nearly reaching or reaching tip, the margin varying from entire to undulate

or crenulate, usually hyaline towards base; filaments presumably white, after anthesis 4-4.7 mm long; gynoecium ellipsoid; ovules 5-6 in each locule, placenta inserted on lower one-half to two-thirds of ovary suture; capsules ellipsoid to ovoid, 10-12 mm long, 5-7 mm in diameter, beaked by styles, including stigmas, 0.8-1.4 mm long; seeds 2-4 in each locule, irregularly ovoid to conic, 4.2-4.7 mm long, 1.3-2 mm in diameter, golden brown to chestnut, rugose-striate, if 3 the middle one often sigmoid.

Occasional on steep hillsides in pine forest, growing in heavy red clay loam. Elevation 2000-2300 m. Flowering late July to the end of August and fruiting September through November. Known from only two collections in the Sierra del Tigre, where seemingly endemic (map 5).

This species is notable for its unusually small, shallowly buried bulb, comparatively long and wide striate scape, short, compact inflorescence, and tepals of unusual shape and texture. To what extent this plant depends upon its rhizome for propagation cannot be determined from the material I have before me. The plants are said to be "occasional", suggesting they tend to grow singly; moreover, the heavy red clay in which they grow could conceivably impede lateral growth of the rhizome. The cells at the inner base of the tepals appear bright green and shiny and are probably nectariferous. Field observation of habit and morphology are needed.

Additional Specimens Examined--

MEXICO

Jalisco: Sierra del Tigre, "3 mi" S of Mazamitla (McVaugh &

Koelz 454, MICH).

6. *Schoenocaulon obtusum* Brinker, Ann. Missouri Bot. Gard. 29: 301. 1942. **Type:** MEXICO. Hidalgo: Pachuca. (Rose & Painter 6722 US, the holotype; GH!, isotype).

Figure 27 & 28.

Bulb ellipsoid to narrowly ovoid, 2.5-3.5 cm long and 1.5-2.3 cm in diameter, enveloped underground by a mat of moderately coarse to coarse brown to dark brown fibers, these forming a neck 7-19 (-27) cm long and 1-1.5 cm in diameter, usually several bulbs attached to a short vertical rhizome and hidden by a seemingly single tunic; leaves 6-9, 30-78 cm long and 4.3-7.5 mm wide, usually longer than the mature raceme, green, 11-12-nerved, the nerves spaced 0.3-0.7 mm apart; scape 25-48 cm long and 2-4 mm in diameter, green to green-purple, the condensed (57-) 70-130-flowered raceme (8-) 11-23 cm long; flowers 4-ranked, when pollen is first being shed pedicelled, the pedicels 0.7-1 mm long and 0.6-1.1 mm in diameter, the uppermost 1-5 flowers often functionally staminate, the raceme usually terminated off-center by a poorly-developed flower; bracts broadly ovate 2-2.7 mm long and 1.5-3 mm wide, membranous to slightly fleshy, dark-brown distally, with 5-7 rust- to dark brown-colored veins, margin minutely crenate to erose; pedicels of nearly mature capsules curving sharply upwards to dispose fruit parallel or nearly parallel to scape, 2-2.5 mm long and 0.8-1.2 mm in diameter, those of any vertical rank 12-19 mm apart; tepals oblong to pandurate, when pollen is first being shed 2.5-3.2 mm long, purple-green to purple, blade fleshy, usually with a median crease, veins obscure, at base, adaxially canaliculate and 0.3-0.8 mm wide, at middle, adaxially canaliculate to plane and 0.6-1.2 mm wide,

at tip blunt to pointed, cucullate and 0.2-0.5 mm wide; hyaline auricles barely perceptible to distinct; nectaries lunate to broadly ovate, 0.3-0.5 mm long and 0.3-0.5 mm wide; tepals continuing to elongate to 3-3.6 mm long; when pollen is first being shed filaments just surpassing tepals, white to pale pink, partially adnate to tepals, continuing to elongate to 3.3-3.6 mm long and becoming magenta; unopened anthers cordate, peach-pink; gynoecium when pollen first being shed plumply ovoid, 2.6-3.3 mm long and 1.6-2 mm in diameter, white to deep magenta; ovules 3-6 per locule, placenta occupying lower two-thirds of ovary suture; when pollen is first being shed styles, including stigmas, 0.4-0.5 mm long; nearly mature capsules plumply ovoid, 10-12 mm long and 5-6.5 mm in diameter, green-purple to straw-colored, beaked by styles, including stigmas, 0.5-0.6 mm long; immature seeds 3-5 in each locule; mature capsules unknown.

Endemic to fir forests near, and open "zacatonales" of Muhlenbergia sp. on, exposed granite outcrops north of Pachuca in Hidalgo (map 5). Elevation approximately 3000 m. Flowering July through September and fruiting September through November.

Originally described by Brinker (1942) from two collections from near Pachuca, Schoenocaulon obtusum, has proven endemic to that region, and is one of the few Schoenocaulon species which grows on granite-derived soil. This species is readily recognizable by its relatively condensed raceme of purple flowers, by the flowers being pedicelled when the pollen is first shed, by fleshy oblong tepals with lunate nectaries, by short filaments which just surpass the tepals,

and by short styles. The purple color which distinguishes this and several other Schoenocaulon species is water soluble and fades over time or if the flowers are boiled. The nectaries become better developed after the pollen has been shed. Moreover, field observations suggest this species may be protogynous.

Additional Specimens Examined--

MEXICO

Hidalgo: Mpio de El Chico, rocky summit of Cerro Zumate, above Pueblo Nuevo (Frame & Galván 249, 270, K, MEXU, NY, UC; Galván 1388, ENCB, UC); El Chico (Lyonnet 329, CAS, MO, NY, US); "Peñas de los Gachupines", above Pueblo Nuevo on road from Real del Monte to El Chico (H. E. Moore, Jr. et al. 4076, A); Sierra de Pachuca (Pringle 13841, GH, MICH).

Figure 27. Schoenocaulon obtusum. Base of plant and inflorescence,
x 0.8 (Frame & Galván 270).



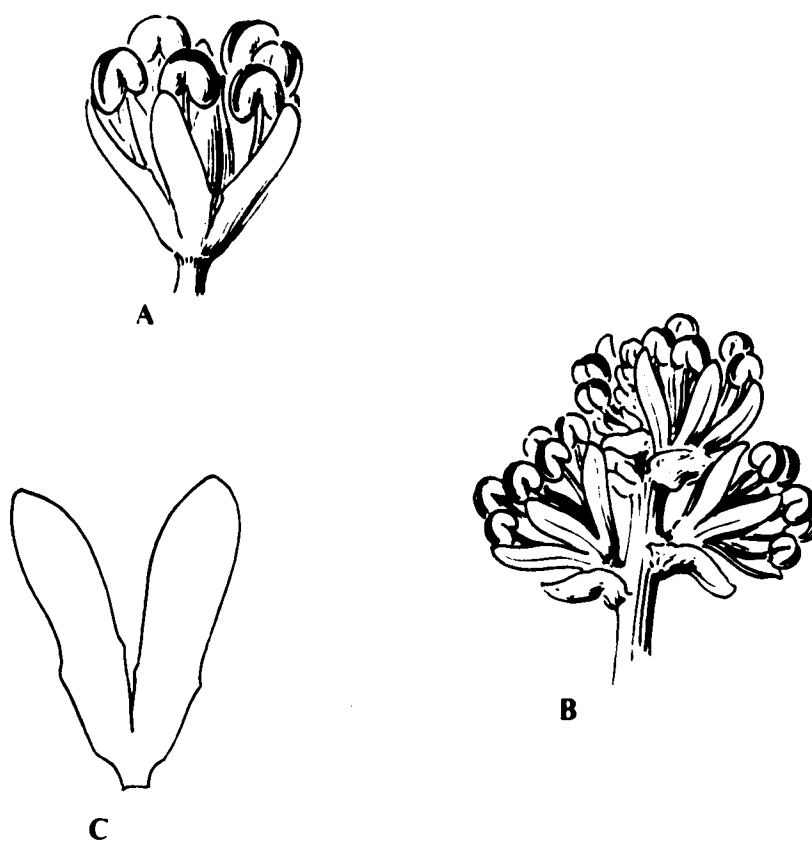


Figure 28. Schoenocaulon obtusum. A, immature flower, x 10; B, detail of termination of inflorescence, x 8; C, outline of two tepals, x 15 (all from Frame & Galván 270).

7. *Schoenocaulon intermedium* Baker, J. Linn. Soc., Bot. 17: 477. 1879. **Type:** MEXICO. Hidalgo: "Mexico prope Zimapan" (Coulter 1570, TCD!, the lectotype; GH!, isoelectotype [Coulter 1569, TCD! probable isoelectotype, see discussion]. Sabadilla intermedia Kuntze, Rev. Gen. Pl. 2: 713. 1891 (as intermedium).

Bulb narrowly ellipsoid to ellipsoid, 3-6 cm long and 1.5-4 cm in diameter, enveloped underground by layers of papery brown leaf-bases to moderately coarse brown fibers, these forming a neck 3-20 cm long and 0.7-2.5 cm in diameter, the rhizome always appressed to the bulb, giving rise to new bulbs vertically, these often hidden by the neck and tunic; leaves 4-7, 22-105 cm long, 2-6.5 mm wide, rigid, varying from shorter than to longer than the mature raceme, often emerging with the inflorescence, at base purple-green, otherwise blade green, usually margin and midrib purple-green, 10-20-nerved, the nerves spaced 0.1-0.4 mm apart; scape 20-60 cm long and 1-4 mm in diameter, magenta to maroon-purple or purple-green, the loose (40-) 50-160-flowered raceme (7-) 9-22 cm long; flowers 3-5-ranked, when pollen is first being shed pedicelled, the pedicels 0.3-0.6 mm long and 0.6-0.8 mm in diameter, the uppermost 8-50 flowers often functionally staminate, the uppermost 30-112 bracts empty or concealing rudimentary flowers often forming a large narrow to triangular crown; bracts pentagonal, 1.5-2 mm long and 1.5-2.2 mm wide, membranous, often pink-purple at base, with 4-5 rust-colored veins, margin crenate; pedicels of nearly mature to mature capsules variable from at an angle perpendicular to scape or slightly curving around scape to curving upwards disposing fruit parallel to scape,

1.2-3 mm long and 0.8-1 mm in diameter, those of any vertical rank 8-15 mm apart; tepals when pollen is first being shed narrowly ovate to lageniform, 1.9-3.2 mm long, maroon-green to purple-green or green-purple, slightly fleshy, at base adaxially canaliculate and 0.4-0.7 mm wide, at middle adaxially canaliculate to plane and 0.4-0.9 mm wide, at tip rounded to pointed and 0.1-0.2 mm wide, auricles indistinct forming raised lateral edges of the channel, nectary apparent as a reniform depression or pit at tepal base, veins 3; tepals continuing to elongate to 2.3-3.4 mm long; when pollen is first being shed filaments surpassing the tepals, subulate, pale pink to magenta, when fully expanded 3.6-5.3 mm long; unopened anthers peach-magenta; gynoecium when pollen is first being shed ellipsoid to ovoid 2.5-3.2 mm long and 1-1.4 mm in diameter, white to deep magenta, carpels nearly free, lightly fused at base through one-half of carpel length; ovules 5-12 per locule, placenta occupying lower two-thirds to three-quarters of ovary suture; when pollen is first being shed styles, including stigmas, 0.4-0.8 mm long; immature capsules bright magenta-purple, mature capsules of two forms, if one- to two-seeded then capsule usually ellipsoid to ovoid, 8-12 mm long and 4-8 mm in diameter, seeds ellipsoid 5.4-6.7 mm long and 1.5-2 mm in diameter, if three- to five-seeded then capsules usually globose, 5-6 mm long and 4-6 mm in diameter, seeds irregularly turbinate to ovoid or trigonal, 3.2-3.8 mm long and 1.4-2.2 mm in diameter; seeds burnt orange to chesnut, and rugose to rugose-reticulate.

Known only from the calcareous hills of the Sierra Zimapán, Hidalgo, and the Sierras de los Alaquines and de Guadalcazár, San Luis

Potosí (map 6). Mostly under trees in open pine-juniper-oak forest or oak forest, sometimes on dry rocky calcareous slopes (then plants of smaller stature), growing in loose calcareous soil with high mineral content. Near Zimapán, the soil ranges in color from orange to purple. Elevation 1600-2380 m. Flowering June through October and fruiting August through November.

Up to this time, no one has had a clear conception of Schoenocaulon intermedium. Baker described S. intermedium from two Thomas Coulter collections (1568, 1570) which were said to have come from Zimapán, a mining town in the state of Hidalgo. I traveled to Zimapán in hopes of finding the Schoenocaulon species which Coulter collected there over a century before. I did not find it on my first visit, but tried again later in the year, and this time found a plant identical to Coulter 1570. A subsequent visit to the Herbarium of Trinity College, Dublin, where Coulter's collections were originally sent from Mexico and later numbered (according to supposed systematic position) and distributed by Harvey, proved very enlightening. I confirmed that the plants I collected near Zimapán were identical to Coulter 1570, and that Coulter 1568, part of the original type, was Schoenocaulon caricifolium. Moreover, I found what appears to be a duplicate of Coulter 1570, labeled by Harvey as Coulter 1569. An additional specimen of Schoenocaulon lacking a label, had "1569?" written in pencil by Harvey (hereafter referred to as Coulter "1569?"). This last specimen is composed of several broken-off inflorescences and a few leaves and is not identical to the TCD specimen labeled Coulter 1569, however, it is identical to what was

distributed by Harvey as Coulter 1569, and to the holotype of Schoenocaulon coulteri Baker (see Schoenocaulon caricifolium discussion). As best as I can reconstruct, it appears that Harvey mislabeled a duplicate of Coulter 1570 as Coulter 1569 (this remained at TCD), and distributed a different collection (and different species) under this number.

I have chosen Coulter 1570 (TCD) as the lectotype for Schoenocaulon intermedium Baker. It is clear from the original description "Spica 3-8-pollicaris deorsum laxiuscula expansa 5-6 lin. diam.", that it formed a part of his conception of the species, in as much as the fully expanded spike of S. caricifolium (Coulter 1568) is no more than 4 inches long. My first choice for a lectotype should have been the specimen of Coulter 1570 from the Kew Herbarium where Baker worked. This specimen is missing and so I made the aforementioned choice of one that may have been seen by Baker.

The following table summarises my knowledge of Coulter's Schoenocaulon collections:

	<u>S. intermedium</u> Baker	<u>S. caricifolium</u> (Schlecht.) A. Gray
TCD	<u>Coulter 1570</u> , <u>1569</u>	<u>Coulter 1568</u> (fruit), " <u>1569?</u> " (fls)
K	<u>Coulter 1570</u> (missing)	<u>Coulter 1568</u> (fruit), <u>1569</u> (fls)
GH	<u>Coulter 1570</u>	<u>Coulter 1568</u> (fruit), <u>1569</u> (fls)

This species is immediately recognizable by this sequence of characters: small flowers which when the pollen is first being shed are shortly pedicellate; perianth of maroon to purple-green or green-purple color; indistinct auricles which form raised lateral edges of the at least basally canaliculate tepals; gynoecium of nearly

free carpels; maroon to green-purple moderately short scape; relatively loose inflorescence; bright magenta-purple immature capsules; small fruits; few moderately narrow and distinctly rigid leaves; and vertically appressed rhizome.

Analysis of whitish material usually found adhering to the tunic of specimens collected by Frame and Tenorio, proves to be a mixture of fungal (possibly actinomyceteous), thin-walled non-septate hyphae, and calcium carbonate crystals (Michelle Seidl and Isabelle Tavares, pers. comm.). It is possible that Schoenocaulon intermedium is endemic to the soils found in the neighborhood of Zimapán, Cárdenas, and Guadalcázar or has a mycorrhizal association with certain fungi, or both.

Additional Specimens Examined--

MEXICO

San Luis Potosí: "Calcareous hills, Cárdenas" (Pringle 3454, F, MEXU); 10 km W of Guadalcázar (Rzedowski 5022, ENCB).

Hidalgo: near Zimapán; 4 km N of turnoff from Mex 85, dirt road to San Francisco (Frame & Tenorio 284, ENCB, GH, K, MEXU, MICH, NY, UC, etc.; Frame & Tenorio 287, ENCB, GH, K, MEXU, MICH, NY, UC, etc.); on trail from Zimapán to mines of El Monte north of Zimapán (H. E. Moore, Jr. et al. 4466, A, MICH).

8. *Schoenocaulon ignigenum* Frame, sp. nov.

LATIN DELIBERATELY OMITTED

Type: MEXICO. Tamaulipas: "between Marcella and Hermosa; burned-over area." (Stanford, Lauber, & Taylor 2626, US! the holotype; DS!, RSA! isotypes).

Bulb ellipsoid, 1-2.5 cm long and 1-2 cm in diameter, enveloped underground by layers of fine to moderately coarse dark brown fibers, these forming a narrow tunic 9-13 cm long and 0.4-1.2 cm in diameter; leaves 3-8, 17-38 cm long and 1.6-3.7 (-5) mm wide, mostly shorter than the scape, green, 8-12 (16-)-nerved, the nerves spaced 0.05-0.3 mm apart; scape 20-40 cm long and 1.5-3 mm in diameter, green to green-purple, usually becoming darker purple toward and within the inflorescence, the moderately loose 67-130-flowered raceme 9-17 cm long; flowers 5-6-ranked, when pollen is first being shed pedicelled, the pedicels 0.3-0.6 mm long and 0.6-1.2 mm in diameter, purple-green, the uppermost 8-35 flowers functionally staminate, the uppermost 6-18 bracts empty or concealing rudimentary flowers and forming a short narrow crown or often this missing and the raceme terminated by a staminate flower; bracts broadly ovate to nearly pentagonal, purple-magenta proximally, 1.5-3 mm long and 2-3.5 mm wide, membranous to slightly fleshy, with 4-7 wine- to rust-colored veins, margin crenate to erose; tepals varying from ligulate to ovate-hastate, 2.4-3.2 mm long, at base canaliculate adaxially and 0.4-0.6 mm wide, at middle plane and 0.6-0.9 mm wide, at tip cucullate and 0.2-0.3 mm wide, distally yellow-green to dark purple and proximally purple-brown to dark purple, usually with a single median vein, rarely 3-veined;

auricles present, the margin usually crenate; filaments when pollen is first being shed just surpassing the tepals, maturing one by one, continuing to elongate to 4.2-4.7 mm, magenta; unopened anthers narrowly sagittate, purple-peach; gynoecium when pollen is first being shed ellipsoid to narrowly ovoid, 2.4-3.4 mm long and 1.3-1.5 mm in diameter, white; ovules 8-13 per locule, placenta occupying lower two-thirds of ovary suture; when pollen is first being shed, styles including stigmas, 0.5-0.7 mm long; nearly mature to mature capsules unknown.

Scattered on rocky limestone hillsides and ridges in open pine forests of the Sierra de Agua de Afuera and adjacent heights in the Sierra Madre Oriental of Nuevo León and Tamaulipas, Mexico (map 7). Elevation 3000-3110 m. Flowering June through August and fruiting August through October.

Endemic to the periodically burned mountain tops of the Sierra de Agua de Afuera and adjacent cerros, Schoenocaulon ignigenum is distinguished by short narrow leaves, short tepals of unusual color with crenate auricles, and short filaments. The tunic in this species provides another important character. As the fine to medium-coarse fibers which thickly envelop the bulb approach the soil surface, they diminish considerably, forming a very thin coat at the soil-surface interface. The change is abrupt and usually occurs a few to several centimeters below the ground level. It is likely that this abrupt thinning of the tunic is related to burning. Either the heat penetrates below the ground, or over time the contractile roots have pulled the bulb deeper underground, or both. As its name implies, the

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species is adapted to regenerate after the lightning fires which occur commonly in the part of the Sierra Madre Oriental to which it is endemic.

Additional Specimens Examined--

MEXICO

Nuevo León: San Onofre, in the district of Zaragoza (Hinton 17581, ENCB).

Tamaulipas: 4 km W of Miquihuana (Stanford, Retherford, & Northcraft 637, DS, GH, MO, NY, UC).

9. *Schoenocaulon plumosum* Frame, sp. nov.

LATIN DELIBERATELY OMITTED

Type: MEXICO. Nuevo León: "shady rock ledges of limestone cliff, Sierra Madre Oriental 21 mi. w. of Linares" (Ripley & Barneby 13565, NY!, the holotype; CAS!, isotype).

Gently tapering bulb ellipsoid to transversely ellipsoid, 1.7-6 cm long and 1.5-5 cm in diameter, enveloped underground by layers of light to dark brown papery leafbases, these forming a neck 7-20 cm long and 0.6-2.2 cm in diameter, of dark brown papery to moderately coarse fibers; leaves 6-11, 47-125 cm long and 2-8 mm wide, green to green-blue, often shorter than the raceme, 10-20-nerved, the nerves spaced 0.2-0.5 mm apart; scape 38-76 cm long, 1.2-4.8 (-5.6) mm in diameter, green at base usually turning brilliant purple to purple-brown toward and within the inflorescence, the moderately condensed (54-) 75-245-flowered raceme 10.5-30 cm long; flowers 5-6-ranked, when pollen is first being shed pedicelled, the pedicels 0.4-1.2 mm long and 0.4-1 mm in diameter, the uppermost one-third to one-half flowers functionally staminate, the uppermost 14-32 (-100) bracts empty or concealing rudimentary flowers and forming a plump to narrow crown; bracts broadly ovate to pentagonal, 1.6-2.6 mm long and 1.9-2.2 mm wide, membranous, with 4-7 wine- to rust-colored veins, margin entire to crenulate or erose; pedicels of nearly mature to mature capsules curving abruptly upwards to dispose fruit mostly parallel to scape, 1.5-2.5 mm long and 0.7-1.1 mm in diameter, those of any vertical rank 9-11 mm apart; tepals varying from distally subulate to ligulate and proximally cuneate to oblong or linear and

nearly lacking auricles, pale green to purple-brown, proximally usually less herbaceous and nearly translucent and distally slightly fleshy, when pollen is first being shed 2-3 mm long, at base adaxially canaliculate and 0.3-0.6 mm wide, at middle plane and 0.4-0.6 mm wide, at tip plane to slightly cucullate and 0.1-0.3 mm wide; nectary appearing as a moderately deep to deep lunate-shaped depression; veins at base 3, the lateral ones often expiring distal to auricles, median vein expiring short of tip; when pollen is first being shed the filaments nearly twice as long as the tepals, white to pale lavender, later usually brilliant magenta or rarely remaining white, when fully expanded 5.5-7 mm long; unopened anthers sagittate, dark magenta, opened anthers dark magenta, often reflexed before abscission; gynoecium when pollen is first being shed narrowly apulliform, 2.5-4.5 mm long and 0.8-1.8 mm in diameter, white to pale lavender, carpels well-sealed; ovules 10-12 per locule, placenta occupying three-fourths to nearly entire ovary suture; when pollen is first being shed styles, including stigmas, 0.4-1.5 mm long; usually gynoecium raised with the filaments to 0.6 mm above the perianth; capsules plumply ellipsoid, 8.2-10 mm long and 3.5-5.3 mm in diameter, often tinged magenta-purple, beaked by styles, including stigmas 0.9-1.3 mm long; seeds 1-2 in each of 2-3 locules, ellipsoid to falciform, 5-6.3 mm long and 1-1.4 mm in diameter, dark red-chestnut, rugose-reticulate, with both ends crowned by a light-brown membranous appendage.

Eastern limestone slopes of the Sierra Madre Oriental in Coahuila, Nuevo León, and Tamaulipas, Mexico, including the outlying Sierras of San Carlos and Tamaulipas (map 7). Growing on steep cliffs

and bluffs in shade under rock ledges or under scrub oaks. Elevation 700-1690 m. Flowering July through October and fruiting August through November.

I was long puzzled by some plants collected near Linares by Ripley and Barneby, and by others collected by myself near Monterey and near the Coahuila/Nuevo León border. When these are seen in context with other plants collected further east and south, a pattern of characters defining a distinct species emerges. Schoenocaulon plumosum is recognizable by papery leaf bases of the bulb, relatively few and generally narrow long leaves, often plume-like inflorescence with one-third to one-half of the upper flowers functionally staminate, flowers with relatively short pedicels, pale green to purple-brown moderately-sized narrow tepals with poorly-defined nectaries, conspicuous purple to brilliant magenta filaments, and plumply ellipsoid fruits of moderate size. Perhaps most likely to be confused with S. macrocarpum or S. madidorum, its near relations, S. plumosum clearly differs by having shorter tepals, and generally fewer, shorter and more narrow leaves. The inflorescence is often flexuous and has a sinuous appearance in specimens. The sinuous inflorescence coupled with the rapid early expansion of white changing to brightly-colored filaments suggests the plume of some exotic bird, and provides the metaphor for this species name.

The flowers of the plants that I collected in Chipinque Park near Monterrey, are strikingly colored. The unopened anthers are deep magenta, the young filaments pale lavender, turning to brilliant magenta as they mature, and the stem pale green. The opened anthers

are dark magenta contrasting sharply with the bright yellow pollen. Most of the pollen is shed rather soon but a little remains in the anther crevices, mostly in the center and along the locular seams, and shows up as a distinctive cruciate design on the anther's abaxial face.

Included in my conception of this species are some plants collected by Stanford et al. (1055) from northwest of El Progreso, Tamaulipas. The collectors note that the plants were growing "On mountains with luxuriant vegetation". The plants are particularly robust, possibly be due to their agreeable habitat.

One specimen, Dressler 2005, shows signs of having survived a fire. As the other specimens which I have examined do not seem to have lived through a burning, natural or otherwise, I suppose that this species is not closely adapted to periodically burned habitats.

Additional Specimens Examined--

MEXICO

Coahuila: near Coahuila/Nuevo León border, dry roadside bank 4.8 km W of La Nogalera on road from Saltillo to Cola de Caballo (Frame 394A, NY).

Tamaulipas: Pico del Diablo, vicinity of Marmolejo (Bartlett 10918, MICH, US); Mpio de Aldama, Los Cerritos to Sierra la Borada (Sierra de San Juan), ca. 40 km NNW of Aldama (Dressler 2005, GH); 10 km NW of El Progreso, which is 18 km NW of Ocampo (Stanford et al. 1055, GH, MO, NY).

Nuevo León: Mpio de San Pedro García, Chipinque Park, near the suburb by the same name which lies just south of Monterrey (Frame

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388, NY); "Dulces Nombres, Nuevo León, and just east of border into
Tamaulipas (Meyer & Rogers 2776, GH, MO); "Trail to Puerta", mountains
near Monterrey (C. H. & M. T. Mueller 12, F); Mpio de Montemorelos,
east slope of Sierra de la Cebolla (C. H. Muller 2885, GH).

10. *Schoenocaulon tenorioi* Frame, sp. nov.

LATIN DELIBERATELY OMITTED

Type: MEXICO. Oaxaca: "El Rodeo, foothills at the southern base of Cerro Verde, NE of Tlacotepec." (Frame et al. 344, NY!, the holotype; K!, MEXU!, UC!, US!, isotypes).

Bulb narrowly ovoid, 1-2 cm long and 1-1.2 cm in diameter, enveloped underground by papery leaf bases, these forming a neck 3.2-7 cm long and 0.4-1 cm in diameter of fine grayish brown to brown fibers; leaves 4-6, 14-24 cm long and 1.5-2.5 mm wide, usually equalling or just surpassing the raceme, green, 7-11-nerved, the nerves spaced 0.1-0.3 mm apart; scape 14-20 cm long and 1-1.6 mm in diameter, barely tapering, straw-colored becoming red-purple to purple-brown towards and within the inflorescence, the loose 12-50-flowered raceme 5-9 cm long; flowers 3-ranked, when pollen is first being shed sessile to subsessile, the pedicels no more than 0.4 mm long, the uppermost 8-10 flowers functionally staminate, the uppermost 2-10 bracts empty or concealing rudimentary flowers and forming a small crown; bracts narrowly triangular to broadly ovate, 2-2.3 mm long and 2.4-2.7 mm wide, membranous, with 6-8 wine-colored veins, margin crenulate to erose; pedicels of mature capsules ascending 45-60° from stem, 0.7-1.2 mm long and 0.7-0.8 mm in diameter, those of any vertical rank 11-14 mm apart; tepals ovate to distally obovate and proximally nearly cuneate, 2.1-2.4 mm long, at base adaxially canaliculate and 0.6-0.8 mm wide, at middle slightly adaxially canaliculate and 0.7-1 mm wide, at tip cuculate blunt to acute and 0.1-0.3 mm wide, blade thick and fleshy, upon rehydration

often with a distal crease, green, green to purple at margin, veins obscure; auricles barely perceptible to each one-third to one-half of tepal length and about one-fifth of tepal width at widest place, margin entire to crenate; nectaries appearing as a distinct lunate to round depression or pit; when pollen is first being shed the filaments just surpassing the tepals, white, when mature 2.5-3.3 mm long, subulate; unopened anthers reniform to cordate, yellow-magenta; gynoecium when pollen is first being shed ovoid, 3.5-3.6 mm long and 1.6-1.7 in diameter, white to white-pink or slightly greenish; ovules 6-7 per locule, placenta occupying lower one-half to two-thirds of ovary suture, carpels loosely cohesive; when pollen is first being shed styles, including stigmas, 0.3-0.6 mm long; capsules plumply ellipsoid to globose, 5-9.5 mm long and 3.2-7 mm in diameter, beaked by styles, including stigmas, 0.3-0.4 mm long; seed(s) 1-2 in each locule, ovoid to conic, 2.8-5 mm long and 1.5-2.2 mm in diameter; golden orange-brown to golden chestnut, striate-rugose to rugose-reticulate.

Open dry rocky hills to the north and south of the Tehuacán Valley in Puebla and Oaxaca (map 1). Growing around scrubby herbs in rocky white limestone. Elevation 1950-2250 m. Flowering July through August and fruiting August through September.

This poorly known species appears to be endemic to the hills rimming the Tehuacán Valley. The plants are distinctly colonial, but because they are small, their colonies are not extensive. The species is immediately recognizable by its small stature, narrow leaves, short loose inflorescence, short pedicels, green fleshy tepals, and small

plumply ellipsoid to globose fruits which are not appressed to the stem. I observed that the plants at El Rodeo were protogynous, with the style and stigma magenta and protruding above the otherwise unopened flower; at this time too, the ovary was relatively large and swollen. Schoenocaulon tenorioi appears to be closely related to S. caricifolium and S. calcicola. Plants from Cerro Verde, the mountain which rises above El Rodeo, seem to represent an aberrant form of S. tenorioi, most being sterile and a few fertile. The material collected by Purpus (Purpus 4389), which comes from Cerro Verde and which closely resembles the plants I collected there, is sterile. The plants from Cerro Verde tend to be a little larger overall and the inflorescence axis rather more pink-purple.

I take great pleasure in naming this species for my friend and collecting companion, Pedro Tenorio Lezama, without whom I would not have been able to learn nearly as much about, nor collect as many, different Schoenocaulon species. Mr. Tenorio is an exceptionally fine collector who specializes in the regions around and adjoining Caltepec, Puebla (his home town), places which earlier had been the haunts of Carl Anton Purpus.

Additional Specimens Examined--

MEXICO

Puebla: Mpio de Vicente Guerrero, 6 km NW of Nicholas Bravo along dirt road to Azumbilla (Tenorio et al. 14128, MEXU).

Oaxaca: Cerro Verde, one days journey by horse from El Rodeo, NE of Tlacotepec (Frame et al. 345, K, MEXU, NY, UC; Purpus 4389, UC).

11. *Schoenocaulon tenue* Brinker, Ann. Missouri Bot. Gard. 29:

304-305. 1942. **Type:** MEXICO. Morelos: "cooler grassy slopes of the knobs of the Sierra de Tepoxtlán, 7500 ft." (Pringle 8356, MO! the holotype; F!, GH!, NY!, POM!, UC!, US!, isotypes).

Figure 29 & 30.

Bulb ovoid to ellipsoid, 1-2.3 cm long and 0.9-2 cm in diameter, enveloped underground by a tunic of fine soft fibers, these forming a neck 4-7.5 cm long and 5-9 mm in diameter; leaves 4-8, 30-45 cm long, 1.2-2.3 mm wide, varying from shorter than, equalling or surpassing the raceme, green to gray-green, 7-9-nerved, the nerves spaced 0.1-0.25 mm apart; scape 17-37 cm long and 0.8-1.6 mm in diameter, barely tapering, the loose 15-35-flowered raceme 7.5-12 cm long; flowers 3-ranked, when pollen is first being shed pedicels 0.3-0.5 mm long and 0.4-0.5 mm in diameter, the 5-12 uppermost flowers functionally staminate, uppermost 2-10 bracts empty or enclosing rudimentary flowers forming a loose crown, or this sometimes lacking and inflorescence terminated by a functionally staminate flower; bracts pentagonal to broadly ovate, 2.3-3.2 mm long and 2-3.6 mm wide, membranous, often with a blush of pink at base, tip blunt to acute, the veins 3-4, magenta- to wine-colored, margin crenulate to erose; pedicels of mature capsules curving upward disposing fruit parallel or nearly parallel to scape, 1.5-3 mm long and 0.8-1 mm in diameter; those of any vertical rank 0.8-2.2 cm apart; tepals when pollen is first being shed 2.2-2.5 mm long, narrowly obovate to distally linear to obovate and proximally cuneate, the auricles well-developed, each usually one-third to one-half of tepal length and

width at its widest place, prior to dehiscence pale pink, thereafter usually turning cream, the blade leathery, pale to dark green and green-purple, at base canaliculate adaxially and 0.3-0.6 mm wide, at middle canaliculate to plane and 0.6-0.8 mm wide, at tip acuminate to blunt, cucullate and 0.2-0.3 mm wide, 3-veined, nectary forming a pit at tepal base; when pollen is first being shed the filaments just surpassing the tepals, white or pale pink, later usually turning magenta, elongating to 2.8-3.4 mm long; the unopened anthers cordate, purple-peach or rarely yellow; gynoecium when pollen is first being shed plumply ampulliform, 1.5-3 mm long and 0.9-1.6 mm in diameter, white, thereafter magenta-purple or rarely pink; ovules 5-8 in loosely-sealed ovules, placenta occupying lower two-thirds of ovary suture; when pollen is first being shed styles, including stigmas, 0.5-0.7 mm long; capsules ovoid to ellipsoid, 7-14 mm long and 3-5.5 mm in diameter, when mature straw-colored with purple streaks, beaked by styles, including stigmas, 0.7-1.2 mm long; seeds 1-3 in each of 1-3 locules; seeds narrowly ovoid to narrowly ellipsoid, 4.6-7.6 mm long, 1.4-1.9 mm in diameter, golden brown to chesnut, reticulate-areolate.

Growing on undisturbed grassy summits of steep-sided volcanic hills peculiar to the region of Tepoztlán, Morelos (map 5). Elevation 2250-2500 m. Flowering August and fruiting September.

Schoenocaulon tenue appears to be endemic to the comparatively old volcanic hill formation found in the neighborhood of Tepoztlán. Plants belonging to this species are among the smallest in the genus and for this reason rarely misidentified. Nonetheless, S. tenue might

be mistaken for Schoenocaulon rzedowskii, another plant of small stature which grows in the nearby states of México and Puebla. S. rzedowskii, however, is a somewhat larger, stouter plant characterized by deeply 2-3-channeled tepals and relatively plump, dense seeds.

Within a population of S. tenue, I observed a few individuals that lacked purple pigment, the tepals being entirely green and the stamens white. Such observations demonstrate that color alone cannot define species in Schoenocaulon.

Additional Specimens examined--

MEXICO

Morelos: summit of Cerro Tepechumulco, belonging to what is locally known as the "Cerros de la Luz y Yaxacomie", 2 kms S of San Juan Tlacotenco, N of Tepoztlán (Frame et. al. 279, ENCB, K, MEXU, MICH, NY, UC, etc.).

Figure 29. Schoenocaulon tenue. Plant in flower, x 0.8 (Frame et al.
279).



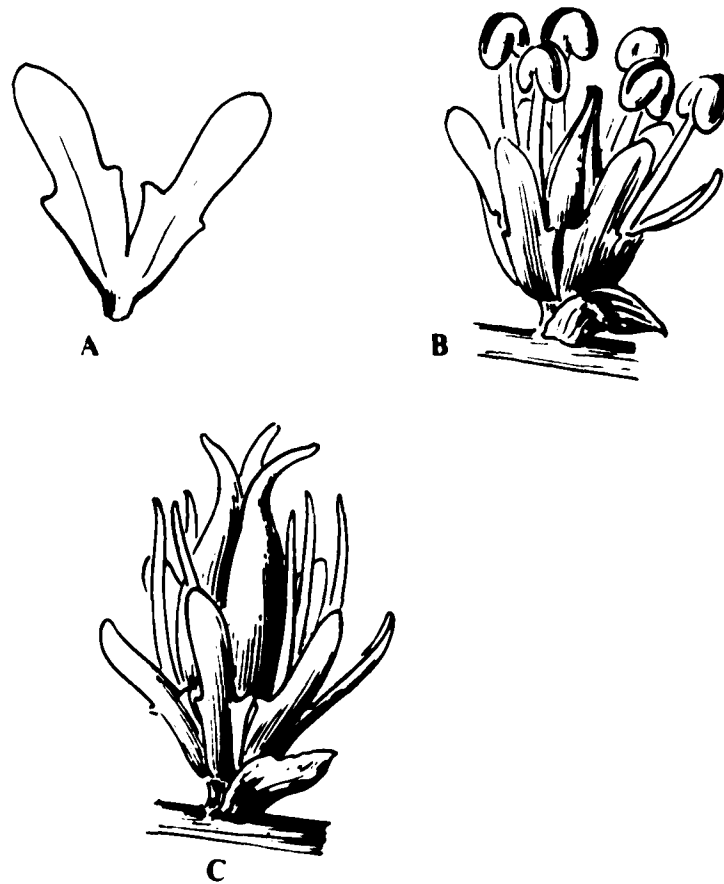


Figure 30. Schoenocaulon tenue. A, two tepals, x 10; B, mature flower shown with unopened anthers, x 10; C, young capsule, x 10 (all from Frame et al. 279).

12. *Schoenocaulon konzattii* Brinker, Ann. Mo. Bot. Gard. 29: 297.

1942. **Type:** MEXICO. Oaxaca: Cerro de San Felipe (Conzatti & González 449, US!, the holotype; GH!, isotype).

Bulb ellipsoid to narrowly ovoid, 2.5-3.5 cm long and 2.3-2.5 cm in diameter, enveloped underground by moderately coarse brown fibers, these forming a neck 10-18 cm long and 1.2-1.8 cm in diameter, the fibers turning light brown above ground; leaves 7-9, 56-90 cm long and 4-7 mm wide, tapering to a point, stiff, approximately equalling the raceme, 11-16-nerved, the nerves spaced 0.3-0.7 mm apart; scape 65-75 cm long, 2.5-4.3 mm in diameter, green to green-purple, the loose 115-170-flowered raceme 20-30 cm long; flowers 6-ranked, when pollen is first being shed pedicelled, the pedicels 0.5-1 mm long and 0.8-1 mm in diameter, often hidden by the clasping bracts, the uppermost one-fourth to one-half of the inflorescence usually functionally staminate, the uppermost 8-25 bracts empty or concealing rudimentary flowers forming a loose crown; bracts irregularly pentagonal to broadly ovate, 2.5-3.2 mm long and 2.8-3.2 mm wide, membranous to slightly fleshy towards center, with 7-9 wine-colored veins, margin at base erose, appearing fringed, otherwise denticulate to crenulate; pedicels of immature capsules curving sharply upwards disposing fruits parallel to scape, those of any vertical rank 16.5-21 mm apart; tepals when pollen is first being shed 3-3.5 mm long, in outline distally linear to obovate and proximally cuneate, green, at base adaxially canaliculate and 0.4-0.6 mm wide, at middle canaliculate to plane and 0.4-0.8 mm wide, at tip cucullate and 0.2-0.4 mm wide, 3-veined, the lateral ones expiring short of tip, the central one nearly reaching

tip; the auricles well-developed, each one-third to one-half blade width and length; nectaries appearing as an oval to rectangular depression 0.3-0.4 mm long and 0.3-0.6 mm wide near tepal base; when pollen is first being shed the filaments twice the length of the tepals, continuing to elongate to 7.3-8 mm long; unopened anthers sagittate; gynoecium when pollen is first being shed ovoid, 3.6-4.2 mm long and 1.3-1.8 mm in diameter; ovules 6-8 per locule, placenta occupying lower two-thirds of ovary suture; when pollen is first being shed styles, including stigmas 0.6-1 mm long; mature capsules unknown.

Apparently endemic to the Cerro de San Felipe, Oaxaca (map 8). Elevation approximately 2000 m. Flowering August through September.

Known only from the type collection, Schoenocaulon konzattii seems to be closely related to Schoenocaulon calcicola, a plant inhabiting the dry limestone hills of the neighboring Mixteca Alta. The two are readily distinguished, as S. konzattii is more robust and has filaments nearly twice as long as S. calcicola. More collections of S. konzattii are needed. After careful study of this plant in the field, the herbarium and the laboratory, it may become practical to treat this taxon as a variety of S. calcicola.

13. *Schoenocaulon comatum* Brinker, Ann. Mo. Bot. Gard. 29: 296.

1942. **Type:** "San Luis Potosí, Mexico" (Schaffner 228, NY!, the holotype; CAS!, F!, MICH!, NY!, POM!, RSA!, UC!, US!, isotypes).

Bulb narrowly ellipsoid to ovoid or plumply falciform, 2.5-4 cm long and 1.5-3 cm in diameter, enveloped underground by a thick mat of very coarse, stiff, chesnut to dark brown fibers, these forming a neck 4.5-32 cm long and 0.7-2 cm in diameter formed at an angle to the bulb; rhizome growing vertically, giving rise to bulbs hidden by the mat of fibers; stiff leaves 6-10, 36-75 cm long and 2-5 mm wide, mostly slightly longer than the raceme, pale green to green, 12-14-nerved, the nerves spaced 0.15-0.5 mm apart; scape 17-47 cm long, 1.2-3.7 mm in diameter, usually purple at base, green to straw-colored above, often turning purple towards and including the inflorescence, the relatively loose 30-105-flowered raceme (6.5-8.5-24 cm long, attenuate; flowers 5-ranked, when pollen is first being shed pedicelled, the pedicels 1-1.4 mm long and 0.7-1.2 mm in diameter, the uppermost 3-25 flowers functionally staminate, the uppermost 5-44 bracts empty or concealing rudimentary flowers, forming a small loose crown; bracts broadly pentagonal to broadly ovate, 1.9-2.6 mm long and 2-3.4 mm wide, translucent, with 3-8 rust- to wine-colored veins, margin crenulate to erose; pedicels of mature capsules 2-3.2 mm long and 0.7-1.2 mm in diameter (for angle relative to stem, see discussion), those of any vertical rank 8-17.5 mm apart, when immature green to purple; tepals plumply spatulate to linear or ligulate, green with a purple margin, when pollen is first being shed 2.5-3.7 mm long, at base adaxially canaliculate and 0.5-0.8 mm wide,

at middle adaxially canaliculate to plane and 0.7-1.0 mm wide, at tip rounded to acute, cucullate and 0.2-0.4 mm wide, blade thick and fleshy, hyaline auricles barely perceptible at margins of channel; tepals often continuing to elongate to 3-4 mm long, three-veined, often obscurely so; nectary apparent as a cordate to rectangular depression or smooth specialized tissue at tepal base; when pollen is first being shed filaments surpassing the tepals, continuing to elongate to 5.5-6.2 mm long, white; unopened anthers cordate to sagittate, purple-peach; gynoecium when pollen is first being shed plumply ellipsoid to ovoid, 2.7-4.3 mm long and 1.1-1.6 mm in diameter, white, later brilliant magenta to purple; placenta occupying most of ovary suture, ovules 7-13 per locule; when pollen is first being shed styles, including stigmas, 0.4-0.9 mm long; capsules plumply ellipsoid to plumply ovoid, 10-13 mm long and 4.7-8.4 mm in diameter, straw-colored to purple, beaked by styles, including stigmas, 0.5-0.9 mm long; seeds 1-3 in each of 2-3 locules, conic to ellipsoid, 5.2-6.5 mm long and 1.8-2 mm in diameter, chesnut brown, furrowed to rugose, a thick knob usually crowning distal end of ultimate seed.

Growing among limestone rocks on open slopes of dry chaparral in the Sierra de San Migelito in south-western San Luis Potosí and in the Sierras of Acatlán and Zapotitlán in Puebla, Mexico (map 9). Elevation 1800-2310 m. Flowering June through July and fruiting August through October.

Although poorly known, S. comatum is amply distinct. Distinguishing features are: coarse stiff horsehair-like fibers that

form the tunic (and for which the species is named); an attenuate inflorescence that is usually about the length of the relatively short scape; and fleshy, spatulate to linear or ligulate fleshy green tepals. In this species the onset of expansion between the flowers occurs just prior to their opening, providing them space in which to assume their characteristic open-campanulate form. One striking feature of S. comatum is how the flowers, and later the fruits, are positioned. The first flowers to open are mostly nodding. As the fertilized ovary begins to enlarge, the pedicels return to right angles to the scape, and finally, when the capsules are nearly mature, they turn up at their distal end to orient the capsules nearly perpendicular to the scape, but not appressed to it. Despite a close relationship to S. texanum, S. comatum is sufficiently distinct to deserve specific recognition. It is possible that in the past S. comatum was a local variant of S. texanum which diverged after becoming isolated. S. comatum displays an interesting disjunct distribution between the hills surrounding San Luis Potosí and the hills of the Sierras Acatlán and Zapotitlán in Puebla. It is possible that the populations were once more nearly continuous but have become separated by the relatively recently formed mountains of the Transverse Volcanic Belt. The southern populations appear somewhat more robust, and generally have slightly larger flowers.

A field note on Schaffner 536 (GH) mentions that the common name for this plant is "matu curros", spanish for "kills lice", referring to a traditional use for cevadilla seeds (see chapter on chemistry and ethnobotany). When I visited the San Migelito mountains in 1985, I

saw no trace of Schoenocaulon comatum. As these mountains are just south of the state capital, the city of San Luis Potosí, it is not surprising that the vegetation they support is quite disturbed. Cattle graze freely, and probably have long done so. The last collection of S. comatum from those hills (that I know of) was that of Pennell in 1934. Nonetheless, it is still possible that the species may be found there today, but only in the remotest places.

Most of the labels that accompany Purpus 2731 give the collection date as June 1908 and the locality as "in the vicinity of San Luis Tultitlanapa"; however, one specimen from the herbarium of the University of California, Berkeley, gives the collection date as July 1907 and the locality as Cerro Mazize. San Luis Tultitlanapa was a hacienda which served as the home base for C. A. Purpus from July to August of 1907 and from April to August of 1908 (Sousa S. 1969). The house in which Purpus lived is still standing and is about 1 km west of San Luis Atolotitlán on the road to Caltepec, Puebla. Specimens described as collected "in the vicinity of San Luis Tultitlanapa" or simply "San Luis Tultitlanapa" may have come from a distance as short as a 10 minute walk from the house, to as long as a six hour ride on horseback (P. Tenorio, in MS). Moreover, Cerro Mazize is just north of San Luis Atolotitlán (P. Tenorio, in MS.). Why the collections are given a single number remains unknown, but as they represent the same species, it is not a material matter.

Additional Specimens Examined--

MEXICO

San Luis Potosí: Chiefly in the region of San Luis Potosí (Parry & Palmer 882, F, GH, MO, NY, US); Sierra de San Miguelito, S of San Luis Potosí (Pennell 17686, GH, US; Schaffner 536, GH, NY).

Puebla: Mpio de Caltepec, Cerro Yeltepec above El Compañía (Frame et al. 347, ENCB, K, MICH, MEXU, NY, UC, etc.); Mpio de San Juan Ixcaquixtla, 11 km SW of S. J. Ixcaquixtla (Frame et al. 348, NY, K, MEXU, MICH, UC; Salinas & Tenorio F-3291; Tenorio & Salinas 11547); San Luis Tultitlanapa (Purpus 2731, F, GH, MO, NY, UC, US); Cerro de Mazize (Purpus 2731 [see discussion], UC).

Oaxaca: Cerro Gato, near Membrillos, SE of Santa Catarina Zapocuila (Frame & Tenorio 421, MEXU, NY).

14. *Schoenocaulon jaliscense* Greenm. Proc. Amer. Acad. 43: 20. 1907.

Type: MEXICO. Jalisco: "cool grassy sides of cañons, near Guadalajara" (Pringle 2938, GH!, the holotype).

Bulb narrowly ellipsoid to ovoid, (2-) 3-5.5 (-7) cm long and 1.7-4 cm in diameter, enveloped underground by a tunic of fine to moderately coarse chestnut to dark brown fibers, these forming a neck 3-15 cm long and 1-2.7 cm in diameter, this often emergent to 7 cm, truncated woody rhizome appressed to one side of bulb; leaves 3-8, (11-) 24-130 cm long, 3.3-7 (-8) mm wide, mostly shorter than the scape, grayish green to blue-green, 8-13-nerved; scape 53-140 cm long and 1.2-4.5 (-8) mm in diameter green to green-purple, rarely branching near the lowermost flower to form a secondary inflorescence, the loose 50-320-flowered raceme 10-53 cm long; flowers 3-6-ranked, when pollen is first being shed flowers sessile (in var. regulare) or pedicelled (in var. jaliscense), when present the pedicels 0.8-1.5 mm long and 0.7-1 mm in diameter, the uppermost 5-25 (-40) flowers functionally staminate and the uppermost 2-20 bracts empty or concealing rudimentary flowers forming a loose crown; bracts irregularly elliptic to broadly ovate, 1.4-2.5 mm long and 1.3-2.8 mm wide, translucent, the veins 6-9, wine to magenta-colored, the margin minutely crenate to erose; pedicels of nearly mature to mature capsules ascending at 45-60° from stem and turning up distally, 0.8-1 mm long and 0.8-1 mm in diameter (in var. regulare) or 2.5-3 mm long and 0.7-1 mm in diameter, occasionally resupinate deflecting the fruits (in var. jaliscense), those of any vertical rank 14-18 mm apart; tepals when pollen is first being shed 1.5-2.8 mm long, oblong

to spatulate, auricles barely perceptible to distinct and one-quarter to one-half as long as blade and mostly one-fourth its width, the blade thick and fleshy, gray-green to blue-green or slightly green-purple, at base adaxially canaliculate and 0.5-0.8 mm wide, at middle slightly canaliculate and 0.7-1.1 mm wide, at tip cucullate blunt to acuminate and 0.2-0.4 mm wide, the veins 3, nectaries appearing as a slight cordate to round depression, later tepals continuing to elongate until 2.2-3.2 mm long and nectaries apparent as a deep pit (in var. regulare) or specialized tissue around prominent veins (in var. jaliscense); filaments when pollen is first being shed surpassing the tepals, white, thereafter turning brilliant magenta, continuing to elongate until 3.7-4.5 mm long; unopened anthers reniform, yellowish green to yellow with a blush of pink; gynoecium when pollen is being shed plumply ellipsoid, 1.6-2.5 mm long and 1.1-1.5 mm in diameter, pale green to green, turning greenish purple as it matures; ovules 7-12 in each locule, placenta inserted on the lower two-thirds of ovary suture; styles, including stigmas, 0.3-0.5 mm long, often protogynous, the receptive stigmas reddish and emergent above the unopened perianth; capsules narrowly to plumply ellipsoid, 8-12 mm long, 3.5-5 mm in diameter, beaked by styles, including stigmas, 0.3-0.5 mm long; seeds 1-4 in each of 2-3 locules; seeds narrowly ellipsoid to semi-lunate, 5-7 mm long, 1-2 mm in diameter, with membranous appendages at both ends, these appendages unequal, the longest usually comprising one-third to nearly one-half total length, golden-brown to chesnut, rugose-striate.

This elegant species is immediately recognizable by its tiny

flowers with tepals of unusual color, delicate long scape, and seeds with distinctive membranous appendages. It is endemic to the pine-oak and pine forests of central and northwestern Jalisco, except for an interesting disjunct population in south-central San Luis Potosí. In contrast to most Schoenocaulon species, S. jaliscense grows in soils of igneous origin which have a relatively low calcium carbonate concentration.

1. Plants relatively large and robust, the inflorescence usually at least 24 cm long; flowers pedicelled when pollen is first being shed; flowering June-Oct. var. jaliscense.
1. Plants relatively small and delicate, the inflorescence no more than 20 cm long; flowers sessile when pollen is first being shed; flowering November-February var. regulare.

Schoenocaulon jaliscense var. jaliscense. S. jaliscense Greenm., as to type.

Figure 31.

In protected places, steep rocky slopes and barrancas in pine forest, 1800-2500 m, flowering June through July in San Luis Potosí and September through October in Jalisco (map 10).

Additional Specimens Examined--

MEXICO

Jalisco: La Peña del Diablo, Cerro de Talcozagua, 4 km east of Tapalpa (Frame & Tenorio 406, K, MEXU, MICH, NY; McVaugh 20577, MICH); barranca bluffs near Guadalajara (Pringle 11853, F, GH, MO, UC, US); west of Bolaños (Rose 2987, GH, NY, US).

San Luis Potosí: El Aguijón, 28 km SSW of Rio Verde (Rzedowski

7703, ENCB).

Characters as given in the key.

There exist sterile specimens from the above and nearby localities, but without flowers or fruit they cannot be named unequivocally.

Schoenocaulon jaliscense var. **regulare** (Brinker) Frame in McVaugh, Flora Novo-Galiciana, Vol. 15: 266-267. 1989. **Type:** MEXICO. Jalisco: "trail from San Sebastián to Real Alto. Loma del Orégano" (Mexia 1702, US! the holotype; CAS!, DS!, F!, GH!, MO!, NY!, UC!, isotypes). Schoenocaulon regulare Brinker, Ann. Missouri Bot. Gard. 29: 304. 1942.

Among grasses on steep slopes in oak, pine-oak or pine forests, on decomposed granite in Jalisco (map 10). Elevation 850-2000 m. Flowering November through February and fruiting January through early March.

Additional Specimens Examined--

MEXICO

Jalisco: Mpio Talpa, entre el filo del encino y carretera a Cuale (R. Glez. 1137, IBUG); Sierra de Manantlán, Senderos desde Arroyo El Chilacayote al cerrito central de Cerro La Piedra Bola (Judziewicz et al. 4948, WIS); near stream, W of San Sebastián, Hacienda del Ototal, Arroyo de los Hornos (Mexia 1823-a, CAS, UC, US); Mpio. Cabo Corrientes, 3-10 km generally E on road to Mina del Cuale, from junction 5 km NW of El Tuito (McVaugh 26349, MICH).

Characters as given in the key.

November to February is an odd flowering time for Schoenocaulon

and points to unusual climatic conditions on mountains of the Pacific slope in western Jalisco.

In Mexia's field book (Archives of the Herbarium of the University of California, Berkeley) she notes that this species is "also found on the trail to La Bufa".

Besides the obvious difference in size between the two varieties, jaliscense and regulare, another important difference occurs in the development of the pedicels and nectaries. In var. jaliscense, the pedicels quickly grow out as the pollen begins to be shed, whereas in var. regulare the flowers remain sessile during this period. As the pedicels grow, the tepals enlarge somewhat, and most of their growth is restricted to the base. As a consequence, the tepals are somewhat thinner and less fleshy there, and the auricles become more elaborate with age. There appears to be a rough correlation between the amount of pedicel growth and tepal expansion. In var. regulare, the small depression accommodating the young nectaries later becomes a deep pit perhaps because there is little pedicel and tepal growth, whereas in var. jaliscense in which both pedicels and tepals continue to expand, the nectariferous cells appear dispersed upon the rather stretched tepal base and its three protuberant vascular bundles.

Most specimens of var. jaliscense and some specimens of var. regulare show signs of having undergone periodic burnings to which pine and pine-oak forest habitats are typically subject.

Figure 31. Schoenocaulon jaliscense var. jaliscense. Base of plant and inflorescence, x 0.75; A, perianth, x 7.5; B, immature flower, x 7.5 (all from Frame & Tenorio 406).



15. *Schoenocaulon megarrhizum* M. E. Jones, Contr. West. Bot. 14: 29. 1912 (as megarrhiza). **Type:** MEXICO. Chihuahua: "Guayanopa Canyon, Sierra Madre Mts" (M. E. Jones, s. n., 23 Sept. 1903, POM!, the holotype).

Bulb ellipsoid to ovoid, 1.5-5 cm long and 1-4 cm in diameter, enveloped underground by a tunic of fine to coarse brown fibers, these forming a neck 3.5-11 cm long and 0.7-2.5 cm in diameter; one side of bulb often exaggerated by a truncated woody rhizome, this either vertically appressed to the bulb or at right angles to it; leaves 5-8, 23-85 cm long, 2.5-5 mm wide, usually shorter than the scape, 10-15-nerved, the nerves spaced 0.1-0.5 mm apart; scape 27-67 cm long and 1-4 mm in diameter, sometimes purplish at base, the loose 42-300-flowered raceme 10-35 cm long, nodding in early flower; flowers 5-7-ranked, salver-shaped at anthesis, when pollen is first being shed pedicelled, the pedicels 0.6-1.5 mm long and 0.7-0.9 mm in diameter, the uppermost 6-50 flowers often functionally staminate and the uppermost 12-75 bracts empty or concealing rudimentary flowers forming a plump to narrow crown; bracts narrowly to broadly pentagonal or broadly ovate, 2-2.8 mm long, 1.5-2.5 mm wide, the veins 4-6, wine-colored, the margin crenate to erose; pedicels of mature capsules 2.8-3.2 mm long and 0.6-1.2 mm in diameter, curving upwards disposing young fruits parallel to scape, those of any vertical rank 12-18 mm apart; tepals when pollen is first being shed 1.7-3.2 mm long, varying from distally linear and proximally cuneate or oblunate to pandurate or plumply lageniform, usually proximally pale green and distally dark green, the proximal half cupping the base of the relatively large

ovary as the outer stamens mature, and the distal half weakly to moderately spreading, at base canaliculate adaxially and 0.3-0.8 mm wide, at middle weakly canaliculate adaxially and 0.5-1.3 mm wide, at tip cucullate, round to apiculate and 0.1-0.4 mm wide, the blade fleshy, the veins 1-3, obscure to distinct, the central nerve often appearing as a median ridge on the abaxial face; auricles barely perceptible to each one-quarter of tepal width at its widest place and two-thirds tepal length; nectary discernable as a smooth depression at tepal base, filaments when pollen is first being shed surpassing the tepals, white, continuing to elongate until 3.6-4.6 mm long, the outer whorl of stamens maturing first; unopened anthers narrowly sagittate, yellow, prior to dehiscence turning peach-purple; gynoecium when pollen is first being shed ampulliform to ovoid, 2-4 mm long and 0.8-1.5 mm in diameter, white, later developing magenta streaks; ovules 5-9 in each locule, placenta occupying lower one-half to two-thirds of ovary suture; when pollen is first being shed styles, including stigmas, 0.5-1.2 mm long; capsules globose, 5.5-7.5 mm long and 5-7 mm in diameter, beaked by styles, including stigma, 0.5-0.7 mm long; seeds 1(2) per locule, plumply falciform, 3.8-5.2 mm long and 2.2-2.6 mm in diameter, dark purplish black, striate to rugose-striate.

This species is recognizable by its moderately long to long scapes, comparatively short leaves, loose and comparatively long many-ranked racemes, relatively short green tepals forming salver-shaped flowers, and white filaments. The lowermost flowers begin to open before the raceme has expanded much, and the period of

expansion lasts well after the flowers have been fertilized. The outer whorl of stamens matures first and the anthers are apt to remain attached to the filaments for a short period after dehiscence, during which time the flowers remain open (i.e., the tepals spread in the distal half.). After both sets of anthers have been shed the perianth closes around the developing fruit. The south-eastern members of this species deserve varietal recognition.

1. Plants relatively large and robust, the inflorescence mostly greater than 20 cm long; plants usually solitary, bulb 3-7 cm long and 2-4 cm in diameter. var. megarrhizum.
1. Plants relatively small and delicate, the inflorescence no more than 18 cm long; plants growing in clumps, bulb 1.5-3 cm long and 1-2.7 cm in diameter. var. deminutum.

Schoenocaulon megarrhizum var. *megarrhizum*. S. megarrhizum M. E. Jones, as to type.

Figure 32 & 33.

Steep slopes in open pine-oak forest among rocks in sandy soil; infrequent and scattered along shady banks and under trees in the Sierra Madre Occidental, from Sonora to Sinaloa, Mexico (map 11). Elevation 1400-1900 m. Flowering mid-August through mid-September.

Additional Specimens Examined--

MEXICO

Sonora: 20 km east of Yecora on road to Maicoba (Frame & Tenorio 401, MEXU, NY).

Chihuahua: about 15 km SW of Yecora on road from Alamos to Yecora, close to Chihuahua/Sonora border (Frame & Tenorio 400, NY);

Sierra Charuco, Río Fuerte (H. S. Gentry 2315, F, GH, MO); Sierra Canelo, Río Mayo (H. Gentry 2515, F, GH, MO, UC); San José de Pinal, Río Mayo (H. Gentry 2591, MO); Nabogame (Laferrière 1231, 1587, UC).

Sinaloa: 1 km W of Los Hornos and 23 km NW of Surutato (Frame & Tenorio 396, NY); Barranca la Manzana, just NW of Los Laureles, 32 km NW of Surutato (Frame & Tenorio 397, MEXU, MICH, NY; H. Gentry 6555, GH, MO, NY).

Characters as given in the key.

All material of var. megarrhizum that I have examined clearly shows signs of having been burned, suggesting that it is adapted to periodic burnings. Indeed, in Sinaloa at Barranca la Manzana where I collected a few plants, the hillside had recently been swept by fire. Although normally solitary and scattered, it appears that var. megarrhizum is becoming increasingly rare as the number of cattle grazing freely in the Sierra Madre continues to grow.

I have observed small bees collecting pollen from the flowers of plants growing near Los Hornos. The distally spreading tepals seem to serve as a crude landing platform for potential pollinators, and the slight differentiation in color may possibly serve as a nectar guide.

Schoenocaulon megarrhizum var. **deminutum** Frame, var. nov.

LATIN DELIBERATELY OMITTED

Type: MEXICO. Durango: Santiago Papasquiario (Palmer 419, GH!, the holotype; F!, MO!, NY!, UC!, US!, isotypes).

Top of the Sierra Madre Occidental in Durango and Nayarit, Mexico (map 11). Growing in pine-oak forest. Flowering August.

Additional Specimens Examined--

MEXICO

Nayarit: Near Santa Teresa, top of Sierra Madre (Rose 2227, NY? [see discussion], US).

Characters as given in the key.

Although the specimens collected from near Santiago Papasquiaro and Santa Teresa are nearly a hundred years old, they clearly represent a different sort of Schoenocaulon megarrhizum than do plants which grow further north and west in the Sierra Madre Occidental. The plants from Durango and Nayarit are united on the basis of their similarity in stature and habit, and in these respects are readily distinguishable from var. megarrhizum. However, as best as I can discern from the available material, the flowers of plants from the two localities are rather different suggesting that the population diverged independently from within S. megarrhizum. As more material becomes available from these two regions, the relationships of these populations to each other and var. megarrhizum may be resolved. The specimens of var. deminutum do not seem to have been burned.

The collection locality for Rose 2227 is given on the US duplicate as "from near Santa Teresa"; however, the label of the NY specimen reads "collected in the state of Durango", which is probably a mistake--see McVaugh, Contributions from the University of Michigan Herbarium, Vol. 9, pages 296-298.

Figure 32. Schoenocaulon megarrhizum var. megarrhizum. Base of plant and inflorescence, x 0.8 (Frame & Tenorio 396).



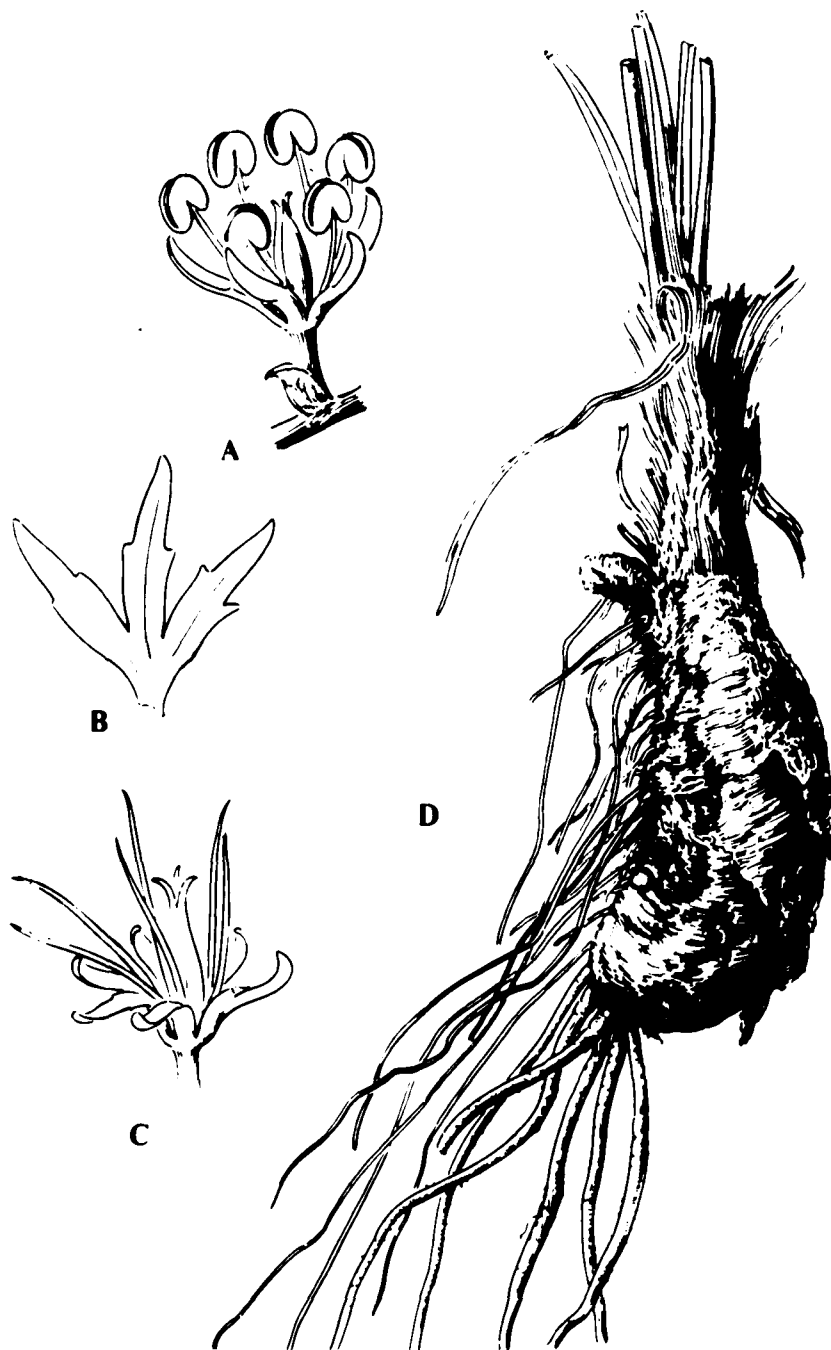


Figure 33. *Schoenocaulon megarrhizum* var. *megarrhizum*. A, immature flower, x 8; B, three tepals, x 12; C, mature flower after anthers have abscised, x 8; D, detail of bulb-rhizome, x 0.8 (all from Frame & Tenorio 396).

16. *Schoenocaulon callicola* Greenman, Proc. Amer. Acad. 43: 19.

1907. **Type:** MEXICO. Oaxaca: "Hillsides, Las Sedas, 6000 ft."

(Pringle 5754, GH!, the holotype; ENCB!, MEXU!, US!, isotypes).

Figure 34 & 35.

Bulb narrowly ellipsoid to narrowly ovoid, 2-5 cm long and 1.3-3.5 cm in diameter, enveloped underground by a thick mat of medium to coarse dark brown fibers, these forming a neck 2.5-16 cm long and 0.7-2.5 cm in diameter; the rhizome always appressed to the bulb, giving rise to new bulbs vertically, these often hidden by the mat of fibers; leaves 4-7, 20-95 cm long and 1.6-4.8 mm wide, rigid, usually equalling or shorter than the raceme, green, (8-) 12-15-nerved, the nerves spaced 0.15-0.5 mm apart; scape 25-65 cm long, 1-3 mm in diameter, usually purple to purple-brown at base becoming green towards and within inflorescence, or sometimes entirely green-purple or purple-brown, flexuous when young, the loose 35-120-flowered raceme 8.5-35 cm long; flowers 4-ranked, when pollen is first being shed pedicelled, the pedicels 0.8-1.1 mm long and 0.6-0.8 mm in diameter, the uppermost 2-25 flowers usually functionally staminate, the uppermost 5-40 bracts empty or concealing rudimentary flowers forming a loose dome or laterally flattened crown or this sometimes lacking; bracts narrowly pentagonal, 1.7-2.2 mm long and 1-1.8 mm wide, membranous, with 6-7 wine-colored veins, margin at base erose, appearing fringed, otherwise denticulate to crenulate; pedicels of nearly mature to mature capsules ascending at 45-60° from stem, 1.7-3.3 mm long and 0.7-1.1 mm in diameter, those of any vertical rank 8-19 mm apart; tepals when pollen is first being shed 2.6-2.8 mm long, in

outline distally subulate and proximally cuneate, spreading in distal half, green to green-purple, at base adaxially canaliculate and 0.4-0.6 mm wide, at middle plane and 0.35-0.8 mm, at tip cucullate and 0.1-0.3 mm wide, 3-veined, the lateral ones expiring short of tip, the central one nearly reaching tip, tepals continuing to elongate to 2.9-3.5 mm long; the cream-colored auricles well-developed, each about one-quarter to one-half of tepal width at widest place and one-third to one-half of blade length; well-differentiated nectary appearing as a deep round to triangular depression 0.3-0.4 mm long and 0.3-0.4 mm wide at tepal base; when pollen is first being shed the filaments surpassing the tepals, white, when mature 3.8-4.2 mm long, occasionally turning pink-purple; unopened anthers cordate, peach-colored; stamens maturing singly, the outer whorl first, anthers abscising soon after dehiscence; gynoecium when pollen is first being shed ovoid, 2.6-3.4 mm long and 1-1.4 mm in diameter, white, thereafter becoming pink; ovules 3-5 per locule, placenta occupying two-thirds of ovary suture; when pollen is first being shed styles, including stigmas, 0.7-1 mm long; capsules globose to urceolate or plumply ovoid, 4-10 mm long and 4-5.5 mm in diameter, not appressed to stem, beaked by styles, including stigmas, 0.7-1.1 mm long; seeds 1(2) in each locule, falciform, 3.5-5.3 mm long and 1.3-1.7 mm in diameter, chestnut to dark brown, striate-rugose, with a light brown ridge running the length of the concave face and crowning the distal tip.

Growing usually singly or in colonies of two or three in leaf litter under or near Juniperus flaccida or Quercus sp., on open eroded slopes of white limestone. This species appears to be endemic to the

dry limestone hills of the Mixteca Alta in northeastern Oaxaca (map 8). Elevation 1950-2350 m. Flowering late June through July, fruiting August through September.

With its long slender loose raceme, comparatively short narrow leaves, small flowers that offer pollen only briefly, small globose to urceolate capsules, and bulb-rhizome reproducing bulbs vertically, this species evidently is well-adapted to the harsh xeric conditions in which it grows. The well-developed nectaries are easily seen when the flowers are boiled. On specimens, nectar is apparent as glistening honey-colored granules found near the tepal base. Although not clearly visible, some nectar may also be produced from the base of the ovary; further investigation of this is needed. As water may be lost by transpiration through open anthers, it is possible that in response both ~~to~~ its xeric habitat and pollinators, S. calcicola has evolved to offer nectar in well-differentiated nectaries and to shed pollen for only a brief period.

Additional Specimens Examined--

MEXICO

Oaxaca: Las Sedas (Pringle 6740, F, GH, MO, NY, UC, US); 1 km north of Telihtlahuaca on road to Las Sedas (Frame et al. 275, ENCB, GH, K, MEXU, MICH, NY, UC, etc.); Disto de Nochixtlán, 1 km al NE de El Paredón, 14 km al SE de Nochixtlán (A. García M. & F. Mérida 2645, MEXU, UC).

Figure 34. Schoenocaulon calcicola. Base of plant and inflorescence,
x 0.8 (Frame et al. 275).

.



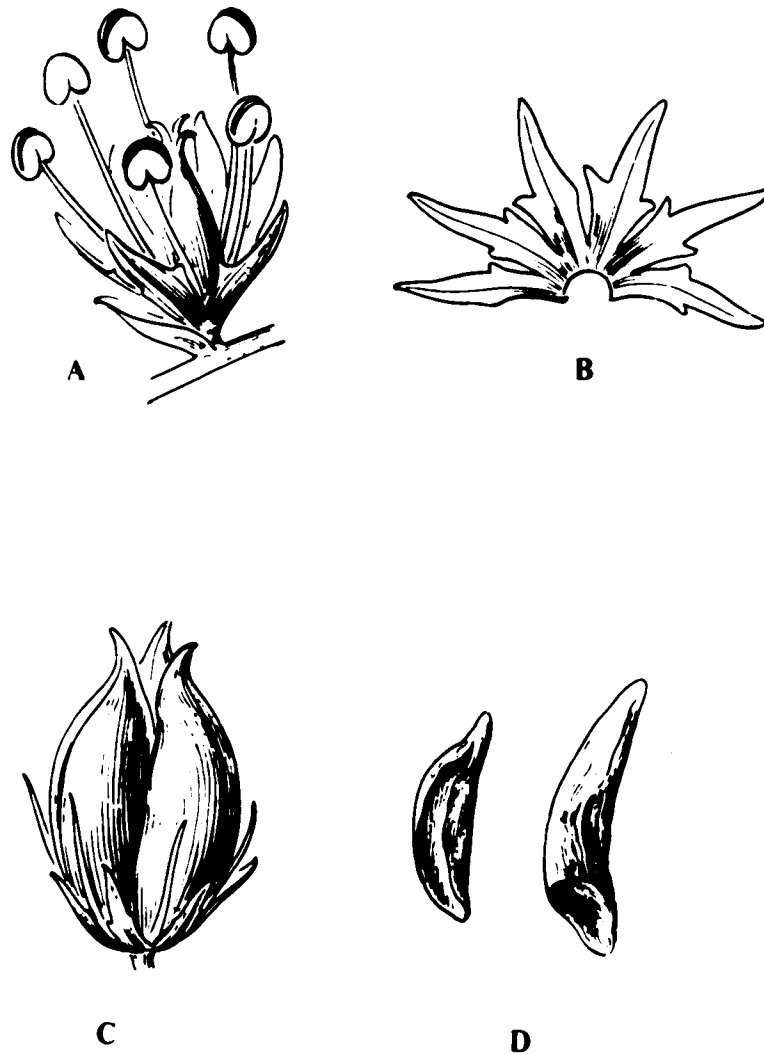


Figure 35. Schoenocaulon calcicola. A, mature flower shown with unopened anthers, x 10; B, perianth, x 10; C, mature capsule, x 6; D, seeds, x 8 (all from Frame et al. 275).

17. *Schoenocaulon dubium* (Michx) Small, Flora South-east. U.S., 250.
 1903. **Type:** UNITED STATES. "Florida" (Michaux s. n., P, the
 holotype, photo of holotype, GH!). Helonias dubia Michaux, Flora
 Boreali-Americana 1: 213. 1803. Schoenocaulon gracile A. Gray, Ann.
 Lyc. New York 4: 127-128. 1837. Sabadilla dubia Kuntze, Rev. Gen.
 Pl. 2: 713. 1891.

Bulb ellipsoid to ovoid, 2-4.2 cm long and 1.2-3.5 cm in diameter, enveloped underground by layers of dark brown papery leafbases, these forming a neck 2.5-17 cm long and 0.5-1.5 cm in diameter of coarse light brown to brown fibers; leaves 4-7, 14-75 cm long and 1.5-3.5 mm wide, shorter than the raceme, green, 8-11-nerved, the nerves spaced 0.1-0.4 mm apart; scape 55-87 cm long, 1-3.5 mm in diameter, purplish at base, otherwise green to straw-colored, the loose 55-220-flowered raceme 11.5-35 cm long; flowers 4-5-ranked, when pollen is first being shed sessile to subsessile, when present the pedicels to 0.3 mm long and 1 mm in diameter, the uppermost 6-35 flowers usually functionally staminate, the uppermost 10-55 bracts empty or concealing rudimentary flowers forming a round to narrow crown; bracts narrowly pentagonal, 1.3-1.7 mm long and 1-1.4 mm wide, membranous, with 5-6 wine-colored veins, margin entire to crenulate; pedicels of nearly mature to mature capsules sharply bent upwards disposing fruit parallel to scape, 0.6-1.4 mm long and 0.7-1.1 mm in diameter, those of any vertical rank 11-19 mm apart; when pollen is first being shed tepals 1.7-2.8 mm long, elliptic to narrowly ovate or obpandurate, green, fleshy, at base slightly canaliculate adaxially and 0.2-0.9 mm wide, at middle plane 0.6-1.1 mm wide, at tip rounded

cucullate and 0.1-0.3 mm wide, spreading when pollen is being shed, thereafter erect and enclosing the ovary, (2-) 3-veined, the veins often converging below tip, tepals usually continuing to elongate to 2-3.2 mm long, often united at base through 0.2-0.5 mm; nectariferous tissue discernable as slight depression at tepal base; filaments when pollen is first being shed nearly twice the tepals, white, after dehiscence of anthers turning magenta, elongating to 3.5-4.8 mm long; the unopened anthers narrowly sagittate; gynoecium when pollen is first being shed ovoid to plumply ovoid, 1.4-2.7 mm long and 0.8-1.5 mm in diameter, white; ovules 7-8 in each locule, placenta occupying one-half to two-thirds of ovary suture; when pollen is first being shed styles, including stigmas, 0.4-0.7 mm long; capsules ovoid, 7.5-11 mm long and 3.2-5.5 mm in diameter, beaked by styles, including stigmas, 0.5-0.8 mm long; seeds 1-3 in each of 2-3 locules, narrowly ellipsoid to ellipsoid, 4-6.3 mm long and 1.3-1.8 mm in diameter, distal end of ultimate seed strongly beaked by appendage, chesnut brown, rugose-striate to rugose-foveate.

Locally abundant in sandy well- to moderately-drained soils in dry pineland and sandhills of Florida (map 12). Elevation sea-level to 50 m. Flowering April through May (sometimes through July) and fruiting June through August.

Schoenocaulon dubium occurs in places subject to annual fires and is apparently adapted to habitats that are periodically burned. Its ability to flower while the bulb is comparatively small suggests that it reaches sexual maturity more rapidly than many other species of its genus. This, in addition to the bulb-rhizome habit, may have led to

its success in such ecosystems. André Michaux in his Flora Boreali-Americana gives the distribution of this species as "in sabulosis Georgiae et Floridae." However, its presence in Georgia has never been confirmed. Like S. ghiesbreghtii, this species inhabits lands that were largely laid down in the Quaternary. I suspect that as nearly all species of the genus are calciphiles to varying degrees, the present distribution of S. dubium is also related to the availability of calcium carbonate in the soil.

S. dubium is perhaps most closely allied to Schoenocaulon ignigenum, which grows in open pine forests of the northern Sierra Madre Oriental of Nuevo León and Tamaulipas, Mexico. Both species are adapted to periodically burned habitats, and share such characters as number and width of leaves, relative tepal shape and size, pedicel length, filament size, and overall aspect. S. ignigenum is, however, generally smaller in stature and has a rather more condensed raceme. For these and other reasons, it is unlikely to be confused with the present species.

Additional Specimens Examined--

UNITED STATES

Florida: Tampa Bay (Alden s. n., NY; 1834, Dr. Burrows s. n., NY; Leavenworth s. n., GH); Putnam Co., near Pomona (18 May 1944, O. Ames, GH); Putnam Co., "High pine land" (J. Barnhart 2082, F, NY); Brevard Co., Eau Gallie (March 1927, H. Beardslee, Jr., UC; Curtiss 6551, GH, MO, NY, US); Brevard Co., Mosquito Lagoon (Curtiss 2900, CAS, F, GH, MICH, MO, NY, US); Brevard Co., Okeechobee region (A. Fredholm 6032, GH, NY); Highlands Co., Archbold Biological Station, 10

mi S of Lake Placid (L. Brass 15340, GH); Broward Co., 30 mi N of Miami (21 March 1942, W. M. Bushwell, WIS); Citrus Co., 0.5 mi N of Inverness (G. Cooley et al. 5942, GH, NY); Citrus Co., 0.5 mi S of Dunellon (Kral 4574, GH); Gilchrist Co., Wilcox (Correll et al. 51674, NY); Volusia Co., Seville (Curtiss 6606, GH, MO, NY, UC, US); Volusia Co., Lake Helen (S. Deam 1671, MICH; 24 April 1911, S. C. Hood, MICH, MO); Volusia Co., (March 1891, Hulst, NY, UC); Volusia Co., Lungren (24 March 1882, Mohr, US; 4 April 1882, Mohr, US); Orange Co., "Dry pine barren" (A. Fredholm 5387, GH, NY); Orange Co., Lake Conway (Huger 13, MO); Alachua Co., Gainesville (March 1876, Garber, F, NY; June 1876, Garber, F, NY, US; 15 June 1910, S. C. Hood, MO; Rev. Lighthipe 479, MO, NY, US, WIS; 30 April 1936, Murrill, MO; 10 July 1936, Murrill, MO); Alachua Co., Santa Fe Lake (1878, H. Gillman s. n.); Alachua Co. (June-July 1898, Hitchcock, F, MO); Alachua Co., SW of main campus, U. of Florida (Wiggins et al. 19866, DS); Lake Co., vicinity of Eustis (June & July 1894, Hitchcock, F, MO; Prof. Marsh s. n., MO; Geo. Nash 297, F, GH, MICH, MO, NY, UC, US; Geo. Nash 1447, US; Geo. Nash 2016, F, NY, US); Lake Co., Lake Brantley (7 July 1894, Lewton, NY); Osceola Co., Lake Gentry (A. H. Howell 1105, US); Hernando Co., Brooksville (Kral et al. 6748, GH, NY; Moldenke 5943, NY; F. Sargent 6040, POM); Fort King & E. Florida (April & May, Leavenworth, NY); Polk Co., E of Lake Marion (J. McFarlin 5261, CAS); Polk Co., Loughman (J. McFarlin 5640, MICH); Marion Co., E of Flemington (Moldenke 1087, MO, NY, US); Pasco Co., St. Joseph (24 April 1927, Rev. H. O'Neill, MO); without definite locality (Buckley s. n., GH, MO, NY; Chapman s. n., MO, US; "from Dr. Torrey 1839", GH;

Ex. Herb. Samuel Hart Wright s. n., DS, NY).

I have before me a specimen from GH which has two printed labels, the upper reads "Ex Herb. George Thurber.", and the lower "Frémont's Expedition to the Rocky Mountains, 1842." The latter label doubtless does not belong to this plant and Greenman has annotated the specimen in pencil to this effect.

18. *Schoenocaulon mortonii* Brinker, Ann. Missouri Bot. Gard. 29:

301. 1942. **Type:** MEXICO. Michoacán: Zitácuaro, Ypasote Hill
(Hinton 13465, MO!, the holotype; GH!, K!, NY!, US!, isotypes).

Bulb ellipsoid to broadly ovoid, 2-4 cm long and 1.5-3 cm in diameter, enveloped underground by a tunic of fine to very coarse brown to black fibers, these forming a neck 5.5-13.5 cm long and 0.7-2 cm in diameter, one side of bulb often exaggerated by the point of attachment to a truncated woody rhizome; leaves 4-12, 32-85 cm long, (2.1) 3-6 mm wide, usually shorter than the raceme, green, 9-13-nerved, the nerves spaced 0.3-0.6 mm apart; scape (26-) 55-120 cm long and 1.4-5 mm in diameter, the loose to slightly condensed 65-250-flowered raceme 11.5-28 cm long; flowers 3-4-ranked, when pollen is first being shed pedicelled, the pedicels 0.5-0.6 mm long and 0.5-0.7 mm in diameter, the uppermost 5-33 flowers functionally staminate, the uppermost 8-50 bracts empty or concealing rudimentary flowers, forming a loose crown; bracts broadly ovate to pentagonal, 1.2-2.1 mm long, 1.4-2.1 wide, the apex sometimes blunt with a point, translucent to slightly opaque, the veins 3-6, wine-colored, sometimes obscure, the margin erose; pedicels of nearly mature to mature capsules 2.5 mm long and 1.2 mm in diameter, those of any vertical rank 8-15 mm apart, disposing flowers at anthesis perpendicular to axis, thereafter strongly curving upwards, disposing mature fruits parallel, or nearly so, to axis; tepals when pollen is first being shed 1.9-3.2 mm long, linear, distinctly auriculate, appearing pandurate in outline, the blade proximally pale green to green and distally green to purple-green, at base deeply canaliculate adaxially

and 0.7-1.2 mm wide, at middle weakly to strongly canaliculate and 0.4-0.8 mm wide, at tip weakly canaliculate or plane, acuminate to apiculate, cucullate and 0.1-0.4 mm wide, the veins 3, the lateral ones expiring short of tip, the central one reaching or nearly reaching tip; nectariferous tissue visible as a slight depression deeply channeled by the veins at tepal base; tepals continuing to elongate until 2.6-3.7 mm long; filaments when pollen is being shed surpassing perianth, white, continuing to elongate until 4.2-5.6 mm long and sometimes turning bright magenta; unopened anthers narrowly sagittate, peach-purple; gynoecium when pollen is first being shed plumply ampulliform, 1.5-1.6 mm long and 0.9-1 mm in diameter; when pollen is first being shed styles, including stigmas, 0.4-0.5 mm long; ovules 4-7 (-11) in each locule, placenta occupying lower one-half to two-thirds of ovary suture; capsules narrowly ellipsoid to narrowly oblong, 9-1.5 cm long and 0.3-0.5 cm in diameter, beaked by styles, including stigmas, 0.9-1.5 mm long; seeds 2-4 in each of two locules, conic to rhomboidal 5-6 mm long and 1.4-1.6 mm in diameter, chesnut brown, undulate to rugose, usually forming membranous appendages at contact points between seeds.

Growing in oak or pine-oak forests in the rich volcanic soils of northeastern Jalisco, Michoacán, and the district of Temascaltepec in southwestern state of México (map 10). Elevation 1600-2200 m. Flowering September through early November and fruiting December through January.

Rarely collected in recent times, Schoenocaulon mortonii is a bit of a puzzle. Plants from Jalostotitlán resemble S. comatum in an

attenuate inflorescence, flower shape, color and texture, and bulb-fibers. However, they have the very long thick scape typical of western Mexican Schoenocaulon species, and are here considered (with reservations) a form of S. mertonii. Towards the southern end of its range, S. pellucidum approaches S. mertonii in the width of the leaf and distance between ranks of flowers. As I have no good representative material in both flower and fruit, I can do little more than guess at the significance of these characters. Schoenocaulon pellucidum is found at low altitudes in tropical conditions growing in red soil. It is perhaps best separated from S. mertonii by its papery bulb scales. On the other hand, S. mertonii inhabits upland areas and appears to be adapted to periodic fire. This last statement is deduced from the bulb tunic which is generally thick and often abruptly terminates with singed black fibers. Schoenocaulon mertonii is recognizable by its long scape which is generally 2-3 times the length of the inflorescence, relatively stiff leaves of moderate width which are mostly shorter than the raceme, flowers with rather large wide bases, usually green to green-purple fleshy tepals with auricles mostly parallel to blade, often brilliant magenta filaments, and narrowly ellipsoid to narrowly oblong capsules with long pedicels.

Brinker named this species for C.V. Morton, who intended to describe Hinton 13465 as a new species, using the epithet montanum. Although Morton annotated several duplicates of Hinton 13465 to that effect, the name was never published.

Additional Specimens Examined--

MEXICO

Jalisco: Summit of the ascent "8 mi" SE of Jalostotitlán, road to San Miguel el Alto (McVaugh 17545, MICH, NY).

Michoacán: 4-4.5 miles NW of Cuautla, road to Los Volcanes (McVaugh 19994, MICH, NY); Northwestern foothills of Cerro Tancítaro, 12 km S of Peribán de Ramos (McVaugh 24869, MICH, NY).

México: District of Temascaltepec, Rincón del Carmen (Hinton 2690, DS, K, NY); District of Temascaltepec, Nanchititla (Hinton 4970, F, GH, K, MO, NY, US); District of Temascaltepec, Comunidad (Hinton 9965, GH, K, NY, US).

19. *Schoenocaulon rzedowskii* Frame, sp. nov.

LATIN DELIBERATELY OMITTED

Type: MEXICO. Puebla: "Cerro Amalucan, cerca de Chapultepec, 8 km al E de Puebla" (Rzedowski 24138, MICH! the holotype; DS!, ENCB!, F!, WIS!, isotypes).

Shallowly buried bulb plumply ellipsoid to ovoid, 1.5-3 cm long and 1.5-2 cm in diameter, enveloped underground by moderately coarse brown fibers, these forming a neck 3-10 cm long and 6-12 mm in diameter; leaves 7-9, 40-55 cm long and 2.5-5 mm wide, usually longer than the raceme, green, (9-) 11-15-nerved, the nerves spaced 0.2-0.4 mm apart; scape 19-42 cm long and (1.7-) 2-4.7 mm in diameter, green to green-purple, the moderately loose to slightly condensed 34-80-flowered raceme 10.5-15 cm long; flowers 5-ranked, when pollen is first being shed pedicelled, the pedicels 0.3-0.4 mm long and 0.4-0.6 mm in diameter, the uppermost 2-30 flowers functionally staminate, the uppermost 6-20 bracts empty or concealing rudimentary flowers forming a poorly-developed crown; bracts broadly ovate 2.3-3.4 mm long and 2.8-3.1 mm wide, membranous, with 5-7 wine-colored veins, margin denticulate to crenulate; pedicels of nearly mature to mature capsules curving upwards to dispose fruit parallel to scape, 1.5-3 mm long and 1-1.5 mm in diameter, those of any vertical rank 12-15 mm apart; tepals distally linear to ellipsoid and proximally cuneate, 3-4.8 mm long, tepals often continuing to elongate during anthesis, green to green-magenta, adaxially canaliculate with 2-3 channels, at base 0.5-0.6 mm wide, at middle 0.4-0.7 mm wide, at tip cucullate and 0.3-0.4 mm wide, strongly 3-veined, the auricles well-developed, each

about one-quarter to one-half of blade width and up to one-quarter of blade length; when pollen is being shed the filaments surpassing the tepals, when mature 4-5.7 mm, and magenta; unopened anthers unknown; gynoeceium when pollen is first being shed 2-2.2 mm long and 1-1.1 mm in diameter; ovules 6-9 per locule, placenta occupying two-thirds of ovary suture; when pollen is first being shed styles, including stigmas, 0.3-0.4 mm long; capsules ellipsoid to plumply ellipsoid, 15-20 mm long and 7-9 mm in diameter, beaked by styles, including stigmas, 0.5-0.7 mm long; seeds 1-3 in each locule, ovoid to conic, 5-7.5 mm long and 2-2.8 mm in diameter, golden chesnut to chestnut or dark brown, rugose to rugose-ruminate.

Hills in the Puebla and Tepeaca valleys in the state of Puebla, and in the southeastern valleys in the state of México (map 13). Rare in disturbed grassy habitat, and abundant in undisturbed sclerophyllous matorral. Mostly growing in black soil with limestone rocks, or sometimes in clay-limestone soil. Elevation 2250-2470 m. Flowering June through July and fruiting July through September.

In the state of Puebla, known recently from a population of approximately 12 individuals (or is it a single clonal colony?) growing in a public park in the suburbs of Puebla and from a much larger population on a cerro east of Tecamachalco. An even smaller colony than the first may be found growing on Cerro Tetzcutzingo in the state of México. In the past, this cerro was a royal Aztec garden, to which favorite plants were brought from elsewhere; however, there is no evidence that Schoenocaulon rzedowskii is not native here. As S. rzedowskii often grows on gentle hills in valleys with equable

climates, places under the greatest pressure of transformation by man, it comes as no surprise that several of its populations are barely surviving in what are now essentially public parks. That many more large populations existed in the recent past is likely. Schoenocaulon rzedowskii is distinguished by its small shallowly buried bulb, stout scape, tepals with 2-3 channels running the length of the blade, proportionately small gynoecium when the pollen is first being shed, and relatively large ellipsoid to plumply ellipsoid fruits with rather plump dense seeds. Continued collecting in undisturbed places in the valleys of Puebla and México will perhaps yield several more populations of this rare species.

Named for Jerzy Rzedowski, who has a deep appreciation of the Mexican flora, this species shares with its namesake the characters of being stout and elusive.

Additional Specimens Examined--

MEXICO

México: Mpio de Texcoco, Cerro Tetzcutzingo, 8 km E of Texcoco (Frame & Galván 245, NY).

Puebla: Cerro Amalucan near Chapultepec, 8 km E of the city of Puebla. Public park on outskirts of city (Frame & Tenorio 387, ENCB, NY); "Manzanilla" (F. Nicolás 5302 [additional label reads "vicinity of Puebla, Bro. G. Arsène no. 5302" but has "collector" scratched out.] US; vicinity of Puebla (Bro. G. Arsène s. n., US [duplicate of F. Nicolás 5302 ?]); Mpio de Tecamachalco, Cerro east of Tecamachalco (Tenorio et al. 14160, MEXU).

20. *Schoenocaulon pringlei* Greenm., Proc. Amer. Acad. Sci. 32: 295.

1897. **Type:** MEXICO. Distrito Federal: "Lava beds, Serrania de Ajusco" (Pringle 6415, US! [US #287870] the holotype; CAS!, ENCB!, F!, GH!, MO!, NY!, UC!, US! [US #932237], isotypes).

Figure 36 & 37.

Bulb narrowly ovoid to narrowly ellipsoid, 1.6-4 cm long and 1-2.8 cm in diameter, enveloped underground by a tunic of fine to coarse brown fibers, these forming a neck 4-17 cm long and 0.7-2 cm in diameter; leaves 4-7, (14-) 20-76 cm long, (2-) 2.5-4.5 (-6) mm wide, usually shorter than the scape, green, 9-11-nerved, the nerves spaced 0.3-0.7 mm apart; scape 24-93 cm long and 2-4.5 mm in diameter, a ring of deep stria forming just below the inflorescence, the condensed 20-60-flowered 2.5-8.5 cm long raceme distinctly spirally arranged; flowers 5-ranked, when pollen is first being shed sessile to subsessile, the pedicels reaching 0.3 mm long, uppermost 1-6 bracts empty or concealing rudimentary flowers; bracts broadly ovate to nearly spherical, 2.6-3.5 mm long and 2.6-3 mm wide, membranous, often with a blush of brown, tip acuminate, the veins 5-7, brown-colored, margin subdenticulate to erose, the pedicels of nearly mature to mature capsules ascending 50-70° from stem, 0.5-1.7 mm long and 1-2 mm in diameter; those of any vertical rank 0.7-1.2 cm apart; tepals when pollen is being shed 3.2-4.5 mm long, ligulate to narrowly ovate or sometimes oblong, often with the hyaline to pale yellow auricles slightly jutting out at sides, auricles each about one-third of blade width and two-thirds of blade length, the blade leathery to slightly fleshy, green when pollen is being shed, thereafter becoming

progressively more yellow, at base canaliculate adaxially and 0.6-1 mm wide, at middle canaliculate adaxially and 1.2-2 mm wide, at tip blunt to acuminate, cucullate and 0.4-1.2 mm wide, 3-4-veined, nectary apparent as deep pit at tepal base; when pollen is first being shed the filaments equalling or just surpassing tepals, 3.2-4.5 mm long, white, when mature 4.5-5 mm long, never exceeding tepals by more than 1.2 mm; the unopened anthers cordate, when first exposed green, thereafter becoming pale yellow; gynoecium when pollen is first being shed narrowly ovoid to ellipsoid, 3.8-4.7 mm long and 1.3-1.8 mm in diameter, green; ovules 4-7 per locule, placenta occupying lower one-half of ovary cavity; when pollen is first being shed styles, including stigmas, 0.5-0.7 mm long; capsules narrowly ovoid to narrowly ellipsoid, 1.1-1.4 cm long and 5-6 mm in diameter, when immature green, when mature straw-colored, beaked by styles, including stigmas, 0.7-0.9 mm; seeds 4-6 (7) per locule, seeds irregularly ellipsoid, 5.2-6.7 mm long, 1.2-1.6 mm in diameter, golden brown, reticulate-areolate.

Occasional among tussock grasses (Muhlenbergia sp.) in open pine woods of the Transverse Volcanic Belt from 2900 to 3300 m (map 14). Flowering late May through early July and fruiting late July through early September.

Schoenocaulon pringlei is remarkable for its very short, compact and distinctly spirally 5-ranked inflorescence, relatively large albeit compressed green to green-yellow flowers with barely emergent stamens, long scape, and few moderately narrow leaves shorter than the scape. As the ovary appears large and swollen prior to anther

dehiscence, it seems likely that this species is protogynous.

Close examination of certain S. pringlei specimens suggests that this species may be adapted to a periodically burned habitat. Considering that it grows at high elevations in grassy pine lands, periodic natural fires are likely. Once a common feature of the vegetation in the vicinity of La Cima, on the border of the states of México and Morelos, S. pringlei is very rare today. Dr. Jerzy Rzedowskii attributes this disappearance to the fact that farmers have been burning the grass lands there every year (pers. comm.). It is possible that although S. pringlei may tolerate occasional burnings, it is unable to survive repeated frequent fires.

Additional Specimens Examined--

MEXICO

Hidalgo: "collected between Somoriel and Las Lajas" [Estación Semorriel or Samorriel--railroad station NW of Singuilucan; and presumably it is Las Lajas, Puebla--a town SE of Ahuazotepec] (Rose 9243, US).

Veracruz: Mount Orizaba (Rose 5690, US).

Distrito Federal: Delegación de Tlalpan, 1.5 km al SE del la Estación La Cima (R. Cisneros 1387, DS, ENCB); lava fields ca. 2 km SSW of La Cima R.R. Station, ca. 1 km N of the Morelos border (Iltis et. al. 214, WIS; Iltis et. al. 214a, WIS); SE slope of Cerro Pelado, 1-2 km N & NW of La Cima R.R. Station (Iltis et. al. 903, WIS); lava fields near Cima Station, (Pringle 11716, F, GH, US; Pringle 13621, CAS, F, GH, MEXU, MICH, US); lava beds, La Cima de Ajusco, (Pringle 13778, CAS, F, GH, MICH, MO, US; Rzedowski 12612, MICH).

Morelos: Mpio de Huitzilac, near the monument to Morelos, 2 km S
of the Morelos/D. F. border (Frame & Galván 247, MEXU, NY; Frame &
Galván 268, MEXU, NY; Galván 1366, ENCB, UC).

Figure 36. Schoenocaulon pringlei. Plant in flower, bar = 3 cm
(Frame & Galván 268).



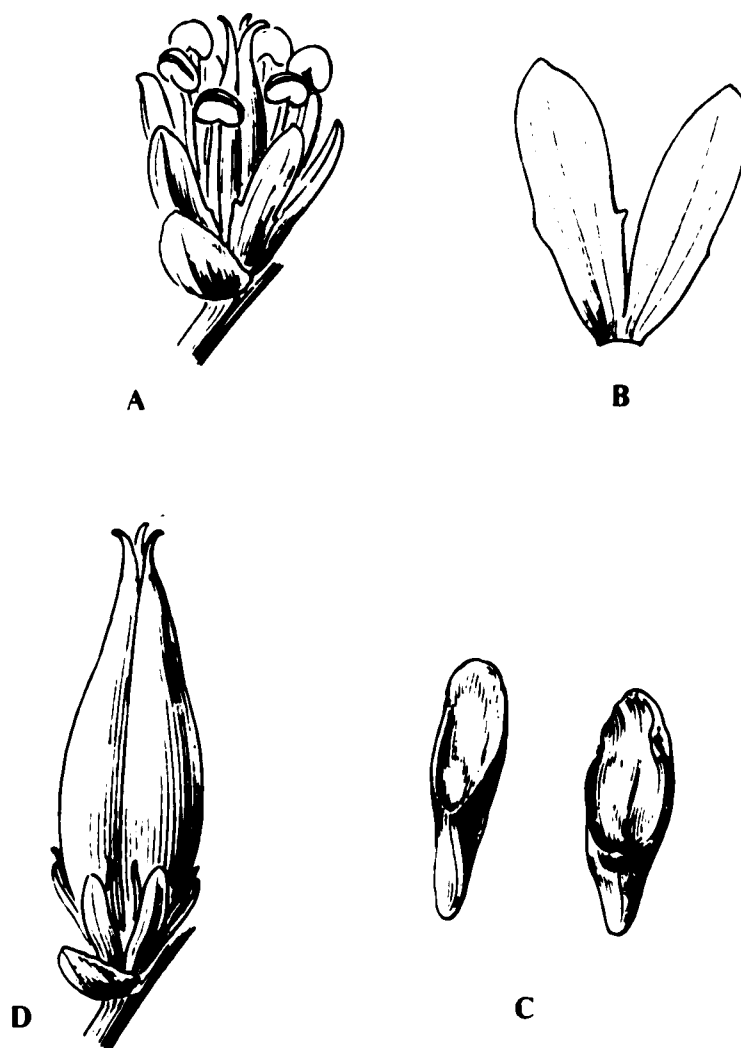


Figure 37. Schoenocaulon pringlei. A, mature flower shown with unopened anthers, x 5; B, two tepals, x 8; C, seeds, x 6; D, immature capsule, x 5 (A-B, Frame & Galván 268; C-D, Frame & Galván 247).

21. *Schoenocaulon caricifolium* (Schlecht.) A. Gray in Hook. & Arn.
 Bot. Beech. Voy. 388. 1840. **Type:** MEXICO. Hidalgo: Near Los Baños
 de Atotonilco el Grande (Ehrenberg, s. n., HAL!, the lectoholotype;
 GH!, HAL! isotypes). [GH!, MEXU!, NY!, POM!, possible isotypes]
Veratrum caricifolium Schlecht., Ind. Sem. Hort. Hal. 8. 1838, Linnaea
 Litt. Ber. 13: 100. 1839. Asagraea caricifolia Kunth, Enum. Pl. 4:
 666. 1843. Sabadilla caricifolia Schlecht., Linnaea 18: 444. 1844.

Schoenocaulon caricifolium Greenman, Proc. Amer. Acad. 43: 19.
 1907. [apparently Greenman was unaware that Asa Gray had already made
 the transfer] **Type:** MEXICO. "without definite locality" (Ehrenberg
 s. n., GH!, the holotype).

Schoenocaulon coulteri Baker, J. Linn. Soc., Bot. 17: 477. 1879.
Type: "Mexico prope Zimapan, Coulter!" (Coulter 1569, K!, the
 holotype; GH!, Coulter "1569?", TCD! [see below and S. intermedium
 discussion] isotypes). Sabadilla coulteri Kuntze, Rev. Gen. Pl. 2:
 713. 1891.

Figure 38 & 39.

Bulb plumply ellipsoid to ovoid, 1.5-3.2 cm long and 1.2-2.5 cm
 in diameter, enveloped underground by layers of dark brown papery
 leaf-bases, these forming a neck 4-15 cm long and (0.4-) 0.7-1.5 cm in
 diameter of almost fine to moderately coarse dark brown fibers; leaves
 7-12, 28-80 cm long, 2.5-5.2 mm wide, longer than the raceme, grayish
 green to blue-green, 8-14-nerved, the nerves spaced 0.25-0.6 mm apart;
 scape 6-30 cm long, 1-4 mm in diameter, the short condensed
 15-65-flowered raceme 4.5-12 cm long; flowers 3-5-ranked, when pollen
 is first being shed sessile or pedicelled, when present the pedicels

1-1.2 mm long and 1-1.2 mm in diameter, the uppermost 1-16 flowers often functionally staminate, the uppermost 2-18 bracts empty or concealing rudimentary flowers forming a crown or often this missing and inflorescence terminated by a staminate flower; bracts broadly ovate 1.8-2.3 mm long, 2.2-2.7 mm wide, membranous and nearly opaque to leathery and opaque, the 5-6 wine-colored veins sometimes obscure, the margin partly entire to wholly erose; pedicels of nearly mature to mature capsules ascending at 10-60° from stem, 1-2.5 mm long, 1-1.5 mm in diameter, those of any vertical rank 8-16 mm apart; tepals when pollen is first being shed 2.4-3.2 mm long, distally ligulate and proximally cuneate (as in var. caricifolium) or broadly falciform (as in var. oaxacense), the blade thick and fleshy, green to green-purple, at base canaliculate adaxially and 0.5-0.7 mm wide, at middle plane and 0.5-1.2 mm wide, at tip rounded to pointed, cucullate and 0.1-0.3 mm wide, 3-veined, sometimes obscurely so; hyaline auricles poorly- to well-developed each about one-third of tepal width at widest place and one-fourth to one-half of tepal length, often irregular in outline, sometimes pinkish, margin entire to crenate; nectary not well-developed, apparent as a deep pit or a shiney smooth nectariferous tissue near tepal base; filaments when pollen is first being shed surpassing the tepals, white, continuing to elongate to 3.7-5.5 mm long; unopened anthers plumply sagittate to testiculate, pale yellow to peach-purple, once open deeply-lobed; gynoecium when pollen is first being shed ovoid, 2.8-5 mm long and 1.5-2.3 mm in diameter, white, becoming pink-purple-colored upon fertilization; ovules 4-6 in each locule, placenta occupying lower one-half to

two-thirds of ovary suture; when pollen is first being shed styles, including stigmas, 0.4-0.8 mm long; capsules plumply ellipsoid to nearly globose, 8-18 mm long, 4-10 mm in diameter, when immature cream-colored with pink streaks, beaked by styles 0.5-1.2 mm long; seeds in uppermost capsules 1-2 per locule, in lowermost 2-5 per locule, irregularly ellipsoid to obovoid and conic, 4-7 mm long, 1.6-3.4 mm in diameter, dark orange-red to chestnut or dark brown, rugose-striate to -reticulate.

One specimen at the Gray herbarium has no label, but a note at the bottom in Asa Gray's handwriting reads: "Ticket lost but I remember it is the *Veratrum caricifolium* Schlecht from Mexico given me by Schlechtendal at Halle 1839". This note, corroborating the fact that the specimen is identical with the type material, has lead me to accept this specimen as an isotype. Moreover, it is probably the material Gray refers to in a letter which was published in The Botany of Captain Beechey's Voyage (p. 388): "The fourth species (*S. caricifolium*) is *Veratrum caricifolium* Schlecht. in Ind. Sem. Halens. of which he has given me a specimen in fine fruit; he possesses young plants raised from the seed also: the foliage, &c., is exactly the same as in the original species, but the spike is shorter and thicker.". Some specimens from Ehrenberg's collection are annotated (in Schlechtendal's own hand) "*Sabadilla caricifolia* Schlecht.", a name not in use until 1844. It is possible that these represent isotypes which were not distributed until at least that date (and I have annotated them as "possibly an isotype") or alternatively that some specimens may have been made from progeny grown in Halle. I have

selected one from among four sheets of beautifully preserved type material from HAL to be the lectoholotype. The label on this specimen was handwritten by Ehrenberg and includes both a short description and a number, viz. 783, which is not found on any other specimen. This possibly represents a collection number, but if so, it remains unclear why it never appears again, for Schlectendal certainly never mentions it.

Schoenocaulon coulteri was described from a Thomas Coulter collection from near Zimapán. In that publication Baker cited no collector's number, although Hemsley (1885) gave the Kew herbarium specimen of Coulter 1569 as the type. This appears to be correct, as Baker was keeper of the Herbarium there, and as the Kew specimen is annotated Schoenocaulon coulteri in his own hand. This specimen is identical with Schoenocaulon caricifolium and the name is here reduced to synonymy; a duplicate of this specimen at the Herbarium of Trinity College, Dublin, is mislabeled "1569?" (see S. intermedium discussion). Moreover, Coulter 1568, GH, K, previously syntypes of S. intermedium (see discussion of S. intermedium), are also identical with Schoenocaulon caricifolium and are here included.

Thomas Coulter resided in Zimapán, Hidalgo, from about January to October, 1827 (McVaugh, J. Wash. Acad. Sci. 33: 65-70. 1943.). It is likely that all his Schoenocaulon collections were made sometime during his sojourn there. However, it is unlikely that he collected S. caricifolium in the immediate neighborhood of Zimapán (S. intermedium grows there), although it is possible that he, or an Indian employee, collected it in or near Atotonilco el Grande. The

specimens, Coulter 1568 and 1569? (TCD), are composed of a few narrow leaves and some broken-off inflorescences, whereas specimens of Coulter 1569 are composed of entire plants with nearly mature to mature capsules. As the material at the Gray herbarium is in rather poor condition and the species is somewhat difficult to identify from incomplete flowering material (characters of the mature fruit being especially helpful), it has taken over a century to properly identify these collections.

This species is recognizable by its short scapes, short condensed inflorescences, large oblong-ellipsoid to nearly globose fruits, and proportionately long narrow grayish green to blue-green leaves. The population of Schoenocaulon caricifolium from Nueva Galicia is the northernmost known and the plants are particularly robust.

1. Plants forming large colonies; flowers pedicelled when pollen is first being shed; tepals distally ligulate and proximally cuneate.

var. caricifolium.

1. Plants forming small colonies of a few bulbs, or growing singly; flowers sessile when pollen is first being shed; tepals broadly falciform.

var. oaxacense.

Schoenocaulon caricifolium var. caricifolium. S. caricifolium
(Schlecht.) A. Gray, as to type.

Rocky calcareous soil in dry open oak woodland along the southern rim of the Central Plateau 2000-3300 m (map 1). Flowering late June through July and fruiting August through mid-October.

Additional Specimens Examined--

MEXICO

Aguascalientes: 2 km E of La Congoja on road to San José de Gracia (Rzedowski & McVaugh 871, MICH, NY).

Querétaro: Mpio de Colón, top of Cerro Zamorano (Rzedowski & McVaugh 429, ENCB, MICH).

Hidalgo: "Zimapan" (Coulter 1569, GH, K, [Coulter "1569?", TCD--see discussion of S. intermedium]; Coulter 1568, GH, K, TCD); 4 kms E of Baños de Amaja--along rocky road to Atotonilco el Grande. Growing near stone pillar on Cerro de los Baños (Frame & Tenorio 283, K, MEXU, MICH, NY, UC, etc.; Frame & Tenorio 288, K, MEXU, MICH, NY, UC, etc.).

Characters as given in the key.

Schoenocaulon caricifolium var. **oaxacense** Frame, var. nov.

LATIN DELIBERATELY OMITTED

Type: MEXICO. Oaxaca: "Distrito Teposcolula--6 Km SW of Tamazulapán along road to Chilapa de Díaz." (Frame & Mendoza 289, NY! the holotype; ENCB!, GH!, K!, MEXU!, MICH!, P!, UC!, US!, isotypes).

Calcareous soil in dry woodland of the Mixteca Alta, Oaxaca (map 1). Growing in leaf litter of scrub oak and madrone. Elevation 2100-2350 m. Flowering May through July and fruiting late July through mid-September.

Additional Specimens Examined--

MEXICO

Oaxaca: Disto Teposcolula, Cerro Llano Redondo, 0.8 km S of Teposcolula (Frame et al. 271, NY; Mendoza 1111, ENCB); slope below

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Pan-Am Highway at Puerto Herrera, just NW of Yanhuitlan (Iltis et al.
1130, WIS); 3 km SW of Tamazulapán on road to Chilapa (Mendoza &
Lorence 715, ENCB, MEXU).

Characters as given in the key.

After repeated examination of the material and analysis of the chromosomes and chemistry (see relevant chapters), I have decided to recognize the Oaxacan representatives of Schoenocaulon caricifolium as a distinct variety, oaxacense. It is likely that the northern and southern elements of the species were at one time more genetically confluent, perhaps before the relatively recent uplift of the Transverse Volcanic Belt. The diversified stable habitats around and within the valley of Oaxaca, have been fertile for speciation of Schoenocaulon.

Figure 38. Schoenocaulon caricifolium. Plant in flower, var. caricifolium, x 0.8 (Frame & Tenorio 288); fruiting spike, var. oaxacense, x 0.8 (Frame et al. 271).



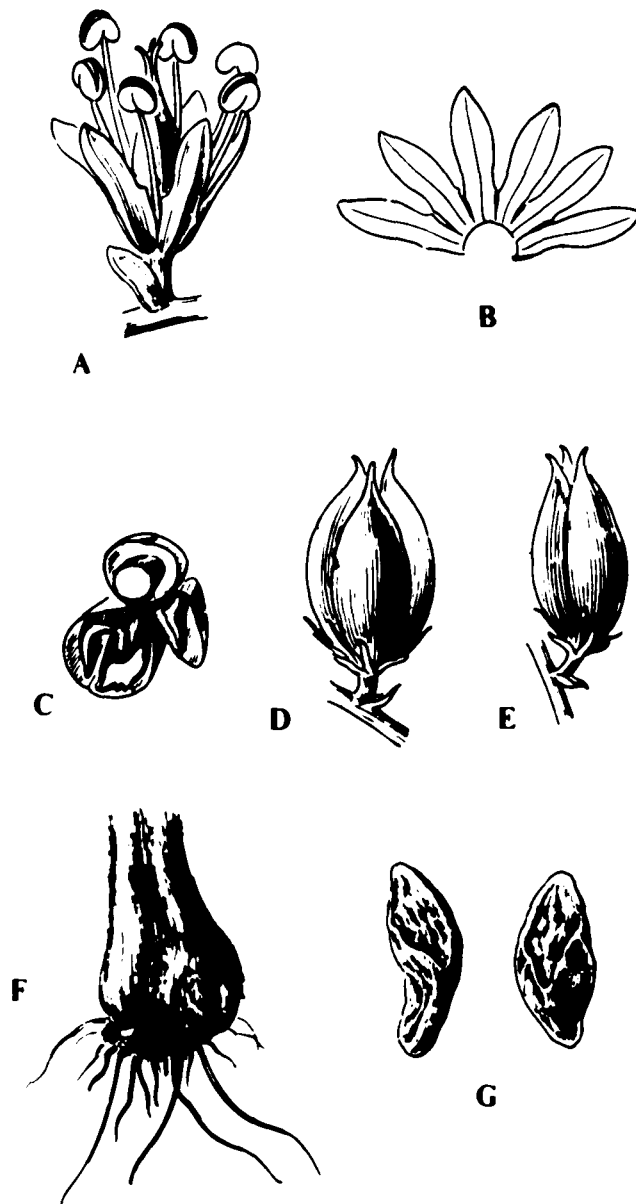


Figure 39. Schoenocaulon caricifolium var. caricifolium. A, mature flower shown with unopened anthers, x 8; B, perianth, x 8; C, cross-section of mature capsule, x 8; D, mature capsule, x 2.5; E, immature capsule, x 2.5; F, detail of bulb-rhizome, x 8; G, seeds, x 4 (A-B & F, Frame & Tenorio 288; C-E & G, Frame & Tenorio 283).

22. *Schoenocaulon texanum* Scheele, Linnaea 25: 262. 1852. Type: UNITED STATES. Texas: "Gesellschaftlich auf trockner Prairie, deren sehr nahe Unterlage Kalkfelsen ist, bei Neubraunfels: Lindheimer. April 1846."

According to Taxonomic literature (Stafleu & Cowan, 1985), the precise location of Scheele's herbarium and types is unknown, although much material is to be found at BREM, GOET, REG, CAS, and the Hermann Roemer Museum in Hildesheim. Scheele received specimens collected in Texas by Lindheimer and described many new species from among them. Lindheimer also was a collector for Asa Gray. Dr. Gray would sort through the material he received from Lindheimer and often request that additional collections be made of particular plants. These were later mounted, labeled and bound together into fascicles and sold under the title Flora Texana exsiccata. I have before me nine specimens with the *Flora Texana exsiccata* label which reads: "543. Fasc. III. leg. F. Lindheimer, 1846." Of these, three have additional handwritten labels which appear to be Lindheimer's original ones, and his collection number, viz. 115. The label at the Gray Herbarium reads: "115. Stony prairies, dry places, sparsely N Br. 4/46 FL". That of one MO specimen reads: "N. 115 Texas April 1846 Zer Streut auf Steiniger trockener Prairie bei N Braunfels. 30 Ex T. Lindheimer". The label on another MO specimen is illegible except for the number "N. 115." It seems likely that these three specimens (GH, MO [207449], MO [207450]) represent isotypes of *S. texanum*, and the remaining six specimens may either be isotypes or material collected later at the request of Asa Gray.

Schoenocaulon drummondii A. Gray ex Torrey, U.S. & Mex. Bound.

Surv. 2: 222. 1859. [nom. illeg.]=Schoenocaulon ghiesbreghtii
Greenman.

Bulb ellipsoid to ovoid or rarely globose, 2-4.5 cm long and 1.2-4 cm in diameter, enveloped underground by layers of dark brown papery leaf bases or moderately coarse to nearly fine medium-brown fibers, these forming a neck 2-17 cm long and 0.5-2 cm in diameter; bulbs usually arranged either in a circle or semicircle around a common rhizome or one above the other on a vertical rhizome; leaves (3-) 5-8, 15-60 cm long and 2-6 mm wide, varying from shorter than the raceme to just surpassing it, rarely much longer than the raceme, pale green to sometimes purplish at base, 8-13-nerved, the nerves spaced 0.2-0.7 mm apart; scape 13.5-55 cm long and 1-4.5 mm in diameter, straw-colored to green-purple usually purple towards and within the inflorescence, the condensed 30-250-flowered raceme 4-32 cm long; flowers 5-6-ranked, when pollen is first being shed pedicelled, the pedicels 0.2-1.1 mm long and 0.7-1 mm in diameter, the uppermost 1-12 (-40) flowers usually functionally staminate, the uppermost 10-60 bracts empty or concealing rudimentary flowers forming a loose, plump to narrow crown, or sometimes this lacking and the inflorescence terminated by a poorly-developed flower; bracts narrowly pentagonal to pentagonal or broadly ovate, pointed, 2-2.7 mm long and 1.5-2.5 mm wide, membranous, often with a greenish-yellow hue, with 4-7 rust- to wine-colored veins, margin crenate to erose; pedicels of mature to nearly mature capsules turned upwards, disposing fruit parallel to scape, 0.5-1.8 mm long and 0.8-1.3 mm in diameter, those of any

vertical rank (5.5-) 8.5-12 mm apart; tepals 2.3-3.8 mm long, linear to distally broadly subulate and proximally cuneate or irregular in outline, blade distally green to green edged with purple and proximally greenish-yellow to green and edged with purple, fleshy, at base canaliculate adaxially and 0.3-0.7 mm wide, at middle plane and 0.4-0.9 mm wide, at tip blunt to acute, cucullate and 0.1-0.4 mm wide, 3-veined, when tepals narrow the lateral veins often obscured by the margin into which they merge distal to tepal base; auricles distinct to absent, when present each approximately one-eighth to one-quarter tepal width at widest place and one-quarter to one-half tepal length, rarely margin irregularly crenate; nectariferous tissue appearing as a shiny smooth surface at tepal base; filaments when pollen is first being shed surpassing the tepals, white to pinkish, continuing to elongate to 4-6 (-7) mm long, and becoming pink-purple; unopened anthers narrowly sagittate, salmon-colored to purple-peach; gynoecium when pollen is first being shed ovoid to ampulliform, 3.2-5 mm long and 1-1.6 mm in diameter, white, becoming streaked with pink upon fertilization; placenta occupying one-half to three-quarters of suture length, ovules (5-) 7-14 (-16) per locule; when pollen is first being shed styles, including stigmas, 0.5-1.3 mm long, unequal; capsules ellipsoid to plumply ovoid, (0.6-) 0.8-1.9 cm long and (2.5-) 5-12 mm in diameter, sometimes elevated with the filaments on a column 0.3-0.6 mm above the perianth (usually if flowers withered or ovules aborted), straw-colored to green-purple or purple, beaked by styles, including stigmas, 0.6-1.5 mm long; seeds 2-4 (-8) in each of 1-3 locules, ellipsoid to ovoid or conic, 3-6.7 mm long and 1.6-2.2 mm in diameter,

orange-red to golden-reddish brown, or grayish-chestnut, rugose to rugose-foveate, with appendages at both ends, a thick nob present at distal end of ultimate seed.

In chaparral on dry rocky limestone soils. usually growing under scrubby vegetation, from south-eastern New Mexico to central Texas, and south to northern San Luis Potosí, Mexico (map 4). Elevation 265-2150 m. Flowering in the United States from late March through June and fruiting from May through September; in Mexico flowering from May through August and fruiting from July through September. Sometimes flowering at later dates following unseasonable rainfall.

Schoenocaulon texanum is recognizable by being colonial, the usually small bulbs often arranged in a circle around a central rhizome; by being usually of small stature (but see discussion below); by a condensed inflorescence; by short pedicels; by relatively small tepals green to green edged with purple; by nectariferous tissue appearing as a shiny smooth surface at the base of the tepal, often near and including a slight depression; and by an ovary with mostly 7-14 ovules per locule, many of which abort so that usually 2-4 seeds per locule are produced.

I here consider how S. texanum varies, some reasons for this variation, how the species differs from others growing in similar habitats, and its circumscription. Schoenocaulon texanum displays a variety of forms, products of age, limited genetic continuity, nutrition, and variable precipitation. In years with plenty of rainfall throughout the generally short rainy season, a mature colony of Schoenocaulon texanum in relatively good soil will attain a rather

larger than ordinary stature and produce an above average number of leaves. It is unclear to what extent the plant's genetic background influences the size of the bulb-rhizome and tunic, although it cannot be disputed that bulb development is related to age and nutrition. The longer the plant lives and photosynthesizes, the larger the perennial storage body, in this case the bulb-rhizome, can grow; and the more robust the bulb-rhizome, the more vigorous the inflorescence. Small bulbs may simply be the result of depletion by browsing herbivores. Nonetheless, in many cases, plants of small stature but of average bulb size can be readily distinguished as the products of a season, or several seasons, of lower than normal rainfall. The hallmarks of such plants are: inflorescences with mature flowers but with little expansion between them, the flowers usually few and often appearing withered and brown, the ovaries often not maturing or, if maturing, perhaps only one unusually small locule ripening to produce a few seeds. Learning to recognize these sorts of variants, and then to include them within one's conception of the species, takes time and experience. Perhaps the easiest way of identifying S. texanum is first to consider where it grows, i.e., in rugged, dry limestone chaparral. Four other species inhabit similar habitats, S. calciola, S. caricifolium, S. comatum, and S. tenorioi. The first differs by a long, loose inflorescence; the second by a broadly ovoid ovary with 2-6 ovules per locule and large-seeded, big plump fruits; the third by a comparatively loose inflorescence which is mostly longer than the scape and a distinctive horse-hair-like tunic surrounding the bulb; and the last by a short loose inflorescence and small globose fruits.

Plants that I collected near Charcas were small, and the flowers were withered by a drought. Furthermore, the land adjoined a goat farm. Elevation also may have an effect upon plant size but, as with other environmental conditions, its precise relation to physiology and genetics remains unknown. Another thesis entirely devoted to the resolution of the limits of this relatively widespread and perplexing species will be required before a satisfactory treatment can be obtained.

Dr. Isabelle Tavares identified a rust fungus from a leaf fragment Cory 51712 (NY) as Puccinia atropuncta Peck & G. W. Clinton (Peck, C. H. 1879. Bot. Gaz. 4: 171. 1879.) According to J. C. Arthur (Manual of the Rusts in United States and Canada, 1934.) the known host genera for the uredinial and telial stages of this rust are as follows: Amianthium, Schoenocaulon, Stenanthium, Veratrum, Zigadenus, and Xerophyllum; and the hosts for the aecial and pycnial stages are Asteraceae: Krigia dandelion and Prenanthes trifoliolatus (Isabelle Tavares, pers. comm.). It is interesting that, with the exception of Xerophyllum, the hosts of the uredinial and telial stages are all members of the Melanthieae, reaffirming the presumptive close relationship of Xerophyllum to this tribe.

Additional Specimens Examined--

UNITED STATES

New Mexico: Otero Co., San Andreas Canyon, Sacramento Mts (7 June 1979, Van Devender et al., ENCB); Eddy Co., Dark Canyon, Rocky Arroyo Rd, Guadalupe Mts, 45 mi SW of Carlsbad (Grassl 71, F, MICH); Eddy Co., Guadalupe Mts (12 May 1939, Hershey, CAS; Hershey 3034, GH);

Eddy Co., NE slope of the Guadalupe Mts, Sitting Bull Falls (Higgins 6721, NY; Higgins 7394, NY); Eddy Co., Guadalupe Mts, along the road east of Queen (Wilkins 2026, US); Chaves Co., 10 miles W of Roswell (28 July 1905, Wooton, US).

Texas: Travis Co., vicinity of Austin ("Biltmore Herbarium" 14799, US; Ertter et al. 4801, NY; E. Hall 644, F, MO, POM, NY, US, WIS; Innes 856, GH; L. Taylor 3271, UC; 16 April 1939, Tharp, CAS, MICH; 28 April 1940, Tharp, F, MO, UC; Tharp 43Q191, MO; Tharp 49259, US; 17 May 1951, Tharp 51-530, ENCB; 25 April 1914, M. Young, MO); Travis Co., Bull Creek (Bogusch 546; US); "Travis Co." (April 1938, Tharp, MO); Bexar Co., Leon Springs (Clemens & Clemens 483, CAS, F, MICH, MO, POM); Bexar Co., vicinity of San Antonio (Sister Metz 2436, F, NY; E. Schulz 792, US); Culberson Co., McKittrick Canyon, Guadalupe Mts (Correll & Johnston 19135, F, RSA, UC; Correll & Hanson 29830, MICH; Meyer & Meyer 2181, MO, NY, UC; Moore & Steyermark 3485, CAS, DS, GH, MICH, MO, NY, UC, US); Culberson Co., head of pass in vicinity of roadside park, Guadalupe Canyon (Correll & Johnston 22004, GH); Culberson Co., 7 miles W of Kent (Correll & Wasshausen 27914, GH, MICH, UC); Culberson Co., vicinity of Frijole Post Office (Grassl 195, MICH); Guadalupe Mts (V. Havard 29, GH); Culberson Co., along Highway 62-180, about 1 mile E of Lamar canyon and 1½ miles SE of Guadalupe Mts Natl. Park boundary (Higgins 17158, NY); Culberson Co., Pine Spring Canyon, about 1 mile above Pine Spring (Hinckley 4449, NY, US); Culberson Co., Guadalupe Mts, south slope of Pine Top Mt (Webster 4577, MICH); Reeves Co., 16 miles NW of Toyahvale, Rte 290 (Correll & Correll 38528, ENCB, UC); Kendall Co., ca. Boerne (Cory 13988, GH; E.

J. Palmer, 9841, DS, MO, US); Kendall Co., 8 miles N of Sisterdale (14 May 1942, Parks, GH); Kendall Co., rocky bluffs, upper Guadalupe (Lindheimer 416, GH, MO); Reverchon 1607, CAS, DS, F, GH, MO, NY, POM, US, WIS); Kendall Co., Comfort (29 April 1940, von Schrenk, MO, WIS); Jeff Davis Co., 17 miles SW of Toyahvale (Cory 17533, GH); Val Verde Co., 10 miles N of Vinegarone (3 May 1942, Cory, GH; 10 May 1942, Cory, GH); Val Verde Co., 30 airline miles N of Del Rio (Cory 41492, GH); Sutton Co., 19 - 20 miles S of Sonora (Cory 41425, NY; Cory 42112, NY); Edwards Co., 25 airline miles NW of Rocksprings (Cory 41490, NY); Blanco Co., $5\frac{1}{4}$ miles W of Johnson City (Cory 51689, NY, MICH); Kerr Co., ca. Kerrville (Cory 51712, DS, MICH, NY, UC, US; Heller 1626, CAS, F, GH, MICH, MO, NY, POM, UC, US, WIS; Pennell 10373, NY); Brewster Co., summit of Old Blue, Glass Mts (Innes et al. 1216, GH); Brewster Co., foothills of Glass Mts, ca. 29 mi S of Ft. Stockton (A. Powell 3596, MO); Brewster Co., near Nichols Ranch House, Glass Mts (Warnock T125, GH, US; Warnock (O. E. Sperry) T625, GH, US); Brewster Co., Baldy Flat (Warnock W82, US); Brewster Co., Altuda Point, 18 miles E of Alpine (Warnock 8451, MICH); Gillespie Co., Nebo Mt (Jermy 329, MO, US); between Kerrville and San Antonio (M. E. Jones 78405, MO, POM, UC); Comal Co., New Braunfels (Lindheimer 711, GH, MO, NY, WIS; Lindheimer 1220, MO; Lindheimer 1221, F, GH, MO, NY, UC, US, WIS); between Mason & Fredericksburg (S. McKelvey 2780, GH); Menard Co., 13 miles E of Menard (McVaugh 8290, DS, F, GH, MICH); Hays Co., San Marcos, rocky uplands (E. J. Palmer 13309, MO, US, WIS; Spring 1899, S. Stanfield, NY); Pecos Co., foothills of Glass Mts, near roadside park, ca. 15 mi from Marathon (A. Powell 3594, MO; Frame 286,

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NY); without definite locality (Oct. 1881, V. Havard, US; C. Wright s. n., GH).

There are several duplicates of C. Wright 697 (GH, UC, US), each with the following label: "Collected in Expedition from Western Texas to El Paso, New Mexico, May--October, 1849, by Charles Wright." The specimen at GH is annotated in pencil "Hays Co., Texas field no 292". B. L. Robinson had a list of Charles Wright's field numbers and corresponding localities (L. Constance, pers. comm.), and the information for the penciled annotation is likely to have come from this list.

MEXICO

Chihuahua: Sierra San Martín de Borracho (M. Johnston et al. 11347, CAS, MEXU, NY); Sierra del Roque, N of Julimes (M. Johnston et al. 12335, CAS, MEXU, NY); Santa Eulalia Mts (Pringle 40, F, GH, MO, NY, RSA, US; 1885, Wilkinson, s. n., NY); 14 km up Cañón del Rayo, northern end of Sierra del Diablo (Stewart 925, GH).

Durango: 5 miles NE of Yerbanis, Mx route #31 (Correll & Johnston 20041, NY).

Coahuila: Sierra Mojada, near Esmeralda (Chiang et al. 9086B, CAS, MEXU; Stewart 1070, GH); Canyon of Sierra la Gavia, 3 km SE of Rancho la Gavia, 4 km S-SW of Santa Genoveva (Frame & Valdés R. 394, GH, K, MEXU, MICH, NY); E slope of Sierra Almagre (H. S. Gentry & Engard 23215, US); Sierra del Pino: vicinity of La Noria (Johnston & Muller 421, F, GH); southwestern end of Sierra de la Fragua, 1-2 km N of Puerto Colorado (Johnston 8754, GH).

San Luis Potosí: Charcas (Lundell 5464, MICH, US; Whiting 523,

DS, MICH, NY, US); Mpio de Charcas, 6 km al E de Laguna Seca

(Rzedowski 6487, DS, ENCB, MICH; Frame & Tenorio 402, MEXU, NY); 5 km

W of Charcas (21 September 1973, Julio Villa, F, WIS).

23. *Schoenocaulon madidorum* Frame, sp. nov.

LATIN DELIBERATELY OMITTED

Type: MEXICO. Puebla: Mpio de Teptetzintla, Cerro

Chiquinahuimazatl, W of Tepetzintla (Tenorio et al. 13851, UC!, the holotype; MEXU, isotype).

Bulb ellipsoid to pumply ellipsoid, 3-4.5 cm long and 2-4 cm in diameter, enveloped underground by layers of papery dark brown leaf bases, these forming a neck 7-20 cm long and 1-2.5 cm in diameter of moderately coarse brown to dark brown fibers, often up to half of the neck emergent; leaves 7-13, 52-100 cm long and (4-) 7-10.5 mm wide, usually equalling or surpassing the raceme, blue-green to green, mostly soft and pliant, 12-13-nerved, the nerves spaced 0.5-1.1 mm apart; scape 20-68 cm long and 1.5-7 mm in diameter, the moderately condensed (35-) 70-200-flowered raceme 14-27 cm long; flowers 4-5-ranked, when pollen is first being shed pedicelled, the pedicels 0.8-1.5 mm long and 0.6-0.9 mm in diameter, the uppermost 15-40 flowers functionally staminate, the uppermost 10-40 bracts empty or concealing rudimentary flowers, forming a small dome crowning the inflorescence, or rarely this missing and the inflorescence terminated by a poorly-formed flower; bracts broadly ovate to pentagonal, 2.4-3.2 mm long and 2-3.5 mm wide, membranous, with 6-7 wine-colored veins, margin crenulate to erose; pedicels of nearly mature to mature capsules usually gently curving upwards to dispose the fruit not quite parallel to scape or sometimes irregularly disposing fruit at right angles to scape, 3-4.5 mm long and 1-1.5 mm in diameter, those of any vertical rank 10-15 mm apart; tepals in outline proximally irregularly

cuneate and distally subulate to linear, green to pinkish green and purple-green, blade fleshy, when pollen is first being shed 2.9-4.1 mm long, at base adaxially canaliculate and 0.4-0.7 mm wide, at middle plane and 0.4-0.7 mm wide, at tip cucullate and 0.15-0.3 mm wide; auricles one-half to two-thirds of tepal width at its widest place and one-third to nearly one-half of tepal length, margin entire to irregularly crenate; when pollen is first being shed nectary varying from a smooth depression to a spherical or cordate pit, later a distinct pit variable in outline, obscurely to distinctly 3-veined, usually one vein visible at blade tip; tepals usually continuing to elongate to 4.2-5.3 mm long; when pollen is first being shed the filaments surpassing the tepals, white, continuing to elongate to 5-9 mm long, turning magenta; unopened anthers sagittate; gynoeceium when pollen is first being shed ovoid to ampulliform, 3.2-4.5 mm long and 1.4-1.6 mm in diameter, white, thereafter often turning pinkish; ovules 4-8 per locule, placenta occupying lower one-half to two-thirds of ovary suture; when pollen is first being shed styles, including stigmas, 0.8-1.1 mm long; capsules plumply ellipsoid to nearly globose, 8-13 mm long and 5-10 mm in diameter, when nearly mature to mature usually raised with the filaments 0.5-0.7 mm above the perianth, beaked by styles, including stigmas, 0.5-1 mm long; seeds 1(2) in each locule, plumply ellipsoid to ellipsoid or conic, 5-9 mm long and 2-3.2 mm in diameter, chestnut, minutely rugose- to reticulate-foveate.

Pine-oak forests in the southern portion of the Sierra Madre Oriental in Puebla, Veracruz, and Oaxaca, Mexico (map 7). Growing

among calcareous rocks in semi-dry to moist places. Elevation 1900-3000 m. Flowering May through July and fruiting June through October.

This species has sometimes been confused with S. officinale, perhaps because it has well-defined nectaries (at least in the later stages of flower maturation) and because the ranges of the two species are nearly coincident in the vicinity of Orizaba, Veracruz. Notwithstanding, S. madidorum is amply distinct. Early on, its nectaries appear as smooth depressions or deep pits near the base of the tepals; later a deep pit is always discernible. These nectaries produce copious nectar which appears in herbarium specimens as honey-like drops on the adaxial surface of tepals. In striking contrast to those of all other species in the genus, the nectaries of S. officinale are distinctive thick pads, presumably formed by the amplification of underlying cell layers. These pads conceal the vascular bundles. I have never seen honey-like drops of nectar on herbarium specimens of S. officinale, and suspect that the nectar is released in rather a different fashion than other Schoenocaulon species.

Schoenocaulon madidorum is fond of moist upland places, for which it is named. The long wide soft pliant leaves, distinctive tepals from which copious nectar is produced, long filaments, striking long pedicels, and plump fruits make it readily recognizable. It is replaced further north by S. plumosum, which grows in drier habitats and which (possibly as a consequence) generally has fewer and narrower leaves, and there are other differences. It is possible that as more

material and information about the two taxa become available, they may be found to represent aspects of a single but somewhat heterogeneous species.

One specimen, Tenorio et al. 14298, has immature capsules parasitized by flies (Diptera: Nematocera), the pupae of which have replaced the seeds. Another fruiting specimen, Hernández et al. 874, has only a few mature capsules intermixed with capsules in which the ovules have all aborted. Pollination studies in this species should be undertaken.

Additional Specimens Examined--

MEXICO

Veracruz: carretera de Puebla a Orizaba, 2 km del bordo con Puebla (J. Fay et al. 754, F); El Paraje, Huayacocotla (R. Hernández et al. 874, MEXU); Maltrata (Matuda 1346, F, MICH, NY, US [Punta de Zacatal, Maltrata (Matuda S-118?, MICH)]); Uluapa, Orizaba (F. Müller 231, NY); Mpio de Huayacocotla, Huayacocotla-Texcatepec (Turra 936, ENCB).

Puebla: Sierra de Zacapoxtla (Diguet s. n., ENCB, MICH); Boca del Monte (Purpus 2490, UC); Mpio Tetela de Ocampo, 8 km al SE de Tetela, brecha a Apulco (Tenorio et al. 14298, UC).

Oaxaca: Distrito de Etla, Cañada de San Gabriel (Conzatti & González 323, GH).

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24. *Schoenocaulon macrocarpum* Brinker, Ann. Mo. Bot. Gard. 29: 300. 1942. **Type:** MEXICO. Nuevo León: "Sierra Madre Oriental; Canyon de los Charcos y Mesa de la Camisa, above Alamar, 15 m. S. W. of Galeana." (C. H. & M. T. Mueller 724, GH!, the holotype; F!, MEXU![see discussion], MICH!, isotypes).

Schoenocaulon lauricola McVaugh ex Frame in McVaugh, Flora Novo-Galiciana 15: 267-268. 1989. **Type:** MEXICO. Aguascalientes: ca. "10 mi" SE of Calvillo [3 hours by horse from Rancho de los Adobes], Sierra del Laurel (McVaugh 18448, MICH!, the holotype; NY!, isotype).

Figure 40 & 41.

Bulb ellipsoid to plumply ellipsoid, 2.5-5 cm long and 2-4.5 cm in diameter, enveloped underground by a tunic of blackish brown papery leafbases or coarse fibers, these forming a neck 5-23 cm long and 1-2.5 cm in diameter of fine to coarse brown fibers; leaves 6-12, 20-100 cm long and 2-8.5 mm wide, varying from shorter than scape to longer than raceme, green, 9-16-nerved, the nerves spaced 0.2-0.75 mm apart; scape (15-) 20-60 cm long and 1.4-6 mm in diameter, varying from green to purple-green and purple-brown, the moderately condensed to condensed 65-275-flowered raceme (9-) 15-26 cm long; flowers 5-8-ranked, when pollen is first being shed pedicelled, the pedicels 0.4-1.1 mm long and 0.7-1.3 mm in diameter, the uppermost 18-50 flowers functionally staminate, the uppermost 1-100 bracts empty or concealing rudimentary flowers, forming a round to narrow crown; bracts triangular to nearly pentagonal, 2.5-4 mm long and 2-3 mm wide, tip sometimes rostrate, membranous, distally often pink, with 4-7

wine-colored veins, margin entire to erose; pedicels of nearly mature to mature capsules curving upwards disposing fruit parallel to scape, 1.5-3 mm long and 0.6-1.2 mm in diameter, those of any vertical rank 7.5-15.5 mm apart; tepals when pollen is first being shed linear to distally linear or subulate and proximally barely cuneate or somewhat oblong, 3-4.2 mm long, pale green to green or yellow-green, at base adaxially canaliculate and 0.3-0.7 mm wide, at middle adaxially canaliculate to plane and 0.4-0.7 mm wide, at tip blunt to acute or rounded, cucullate and 0.1-0.2 mm wide, blade fleshy, three-veined, the veins sometimes only visible at base and when well developed often forming there; auricles barely perceptible to discernable, when obvious each about one-fourth to one-third of tepal length and width at its widest place; nectary appearing as a smooth to channeled depression or pit at tepal base; when pollen is first being shed filaments surpassing tepals, white or brilliant magenta, continuing to elongate to 4.6-6.8 mm long; unopened anthers reniform or plumply cordate, yellow-rose, opened anthers dark rose-purple-brown; gynoecium when pollen is first being shed ellipsoid to ovoid, 2.6-5 mm long and 1-1.5 mm in diameter, white, becoming green to green-pink when fertilized, raised with the filaments above the perianth on a column 0.3-0.7 mm long and 0.6-0.7 mm in diameter, later column continuing to elongate to about 1 mm; ovules 5-12 per locule, placenta occupying lower one-half to three-quarters of ovary suture; when pollen is first being shed styles, including stigmas, 0.8-1.2 mm long, usually unequal, thereafter often spreading to strongly reflexed; capsules narrowly ovoid acuminate or oblong, 9-18 mm long and 3.5-9 mm in

diameter, beaked by styles, including stigmas, 2-3 mm long or these often broken off; seeds 1-2 in each of 2-3 locules, narrowly ellipsoid to semi-lunate, 6.5-8 mm long and 1.3-2.8 mm in diameter, golden-brown to golden-chestnut-brown, rugose-striate to undulate, light brown-colored appendage crowning distal end of seed.

Growing mostly in rich black soil and leaf litter overlying limestone in tall pine/scrub-oak/madroño, pine-oak or oak forests on the western slopes of the northern Sierra Madre Oriental in Coahuila and Nuevo León and the western rim of the Central Plateau in Durango and Aguascalientes, Mexico (map 7). Elevation 2250 to 3200 m. Flowering late May through September and fruiting June through October.

Brinker described Schoenocaulon macrocarpum from a single collection in early fruit. Since that time, several more collections have been made, and a better understanding of its nature and character has been gained. I did not locate S. macrocarpum at "Mesa de la Camisa" (now known as Cerro las Camisas), but found it on an adjacent cerro. Several days later, I collected an unusual, large Schoenocaulon sp. in flower, growing on Cerro Viga near Jamé. It took me a while to realize that this was the same species. Schoenocaulon macrocarpum is recognizable by its many-ranked moderately condensed to condensed inflorescence, long green fleshy tepals with relatively short pedicels (in early flower), column that elevates the filaments and gynoecium above the perianth, spreading to reflexed long styles (including stigma), and generally long narrow ellipsoid fruits. In 1985 and 1986, the years I collected in northern Mexico, severe

drought affected many localities, whereas other neighboring regions were unaffected. This precipitation pattern appears to be cyclic over many years time and may account for some of the variation found in size and number of mature fruit. The plants collected at and near the type locality, a region which often experiences drought, are rather depauperate, and have only a few fruits maturing here and there along the raceme. In contrast, plants from cerros which remain moist throughout the flowering season produce healthy fruits from nearly all flowers. It seems that the species decidedly prefers a rather moist habitat. Note, too, that plants from the type locality and nearby grow at the lowest elevation in that part of the species' range. Earlier I mistook a disjunct population of Schoenocaulon macrocarpum from the Sierra del Laurel in Aguascalientes as representing a distinct species, and described and published it as S. lauricola (see McVaugh 1989). It seems likely that the disjunction occurred after the formation of the Sierra Madre Occidental in the mid-Tertiary (Oligocene to Miocene) which changed the climate drastically and led to the creation of very arid conditions in the Central Plateau (Rzedowski 1983). We see a somewhat similar distribution pattern with S. jaliscense, doubtless for the same reason.

Although the inflorescence is crowded, the flowers are so staggered that they can open wide. As the inflorescence expands, flower by flower, the showy white filaments mature in rapid succession, followed by anther dehiscence. The pedicels are fairly short, but the ovary and filaments are raised above the perianth, exposing the rather poorly developed nectaries. All in all, it is an

alluring display and must catch the attention of more than one insect. The immature green-purple to green-indigo fruits progressively expand until they are nearly rectangular, and are similar to the immature fruits of many Zigadenus species. The distal sutures appear to be under some tension. However, when the capsule reaches maturity, the tension is released as the valves spring apart and reflex.

The specimen at MEXU which I cite as an isotype has an anomalous label which: lacks the collector's name and day of collection; is written in Spanish, and gives the locality in kilometers rather than miles. Moreover, the number "956" has been entered in pencil, but does not seem to bear any relationship to the anonymous collector (it is possibly the MEXU genus number?). It seems likely that the original label was replaced by one from the Mexican National Herbarium, and that some of the original information was not transferred. Abisaí García M. (MEXU) has annotated the specimen as an isotype of Schoenocaulon macrocarpum Brinker.

Additional Specimens Examined--

MEXICO

Durango: Mpio del Mezquital, near La Escondida, on road to Los Charcos (Jiménez & Acevedo 52, ENCB).

Coahuila: Mpio de Arteaga, Cerro Viga, 8.6-14.1 km SE of Jamé, along private road to summit (Frame 393, ENCB, GH, K, MEXU, MICH, NY, UC, etc.); Mpio de Arteaga, "Sierra de Medio Escondida-Arteaga" (Lyonnet 3991, MEXU); Sierra Coahuilón (McDonald 1776, NY); rd past San Antonio, ca. 30 mi E of jct Rte 57 (Pinkava et al. P13577, ENCB, MEXU).

Nuevo León: summit of Mt Infernillo, 9.5 mi S of Pablillo and 19.2 mi S of Mex. 60 (Bell & Rice 17868, MICH, UC); Mpio de Galeana, Cerro las Aguilas [adjacent to Cerro las Camisas], 5 km SE of Alamar along rd from Alamar to Agua Blanca & San Juancito (Frame 390, K, MEXU, NY, UC); "Cieneguillas", Pablillo, SE of Galeana (Pennell 17096, GH, US).

Figure 40. Schoenocaulon macrocarpum. Base of plant and inflorescence, x 0.8 (Frame 393).



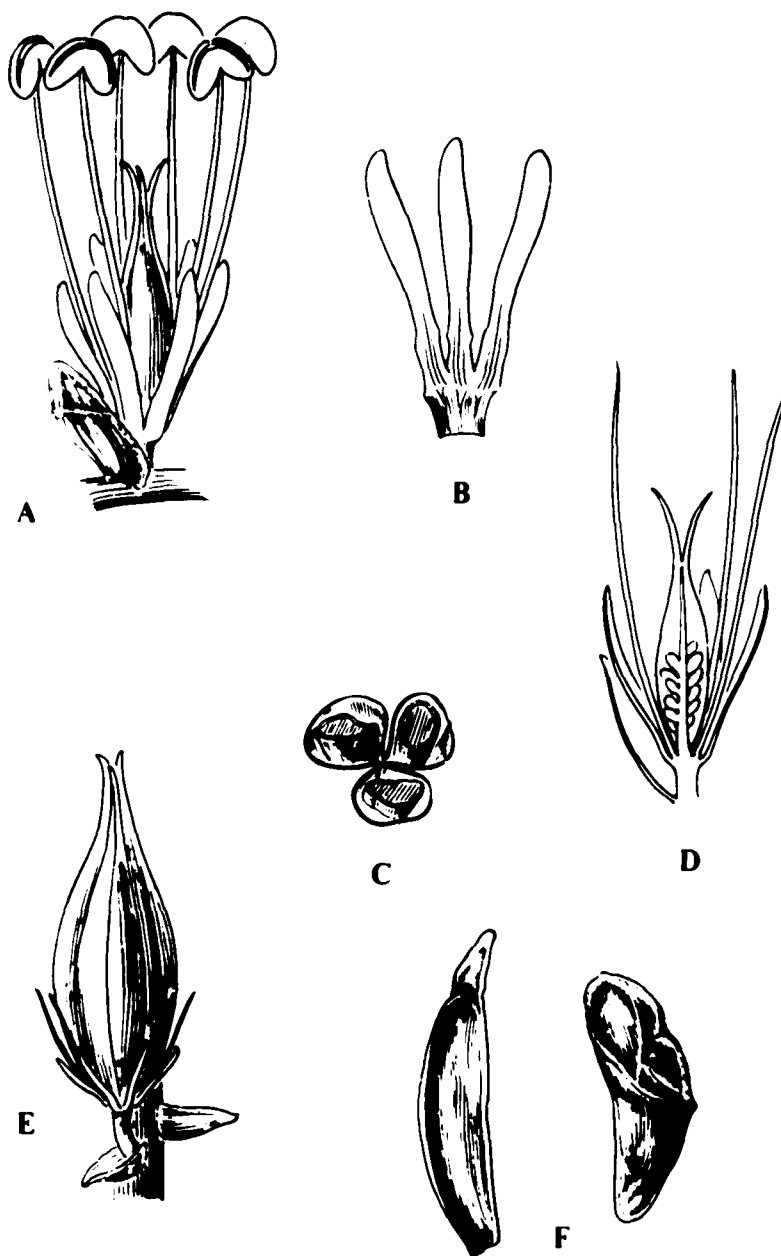
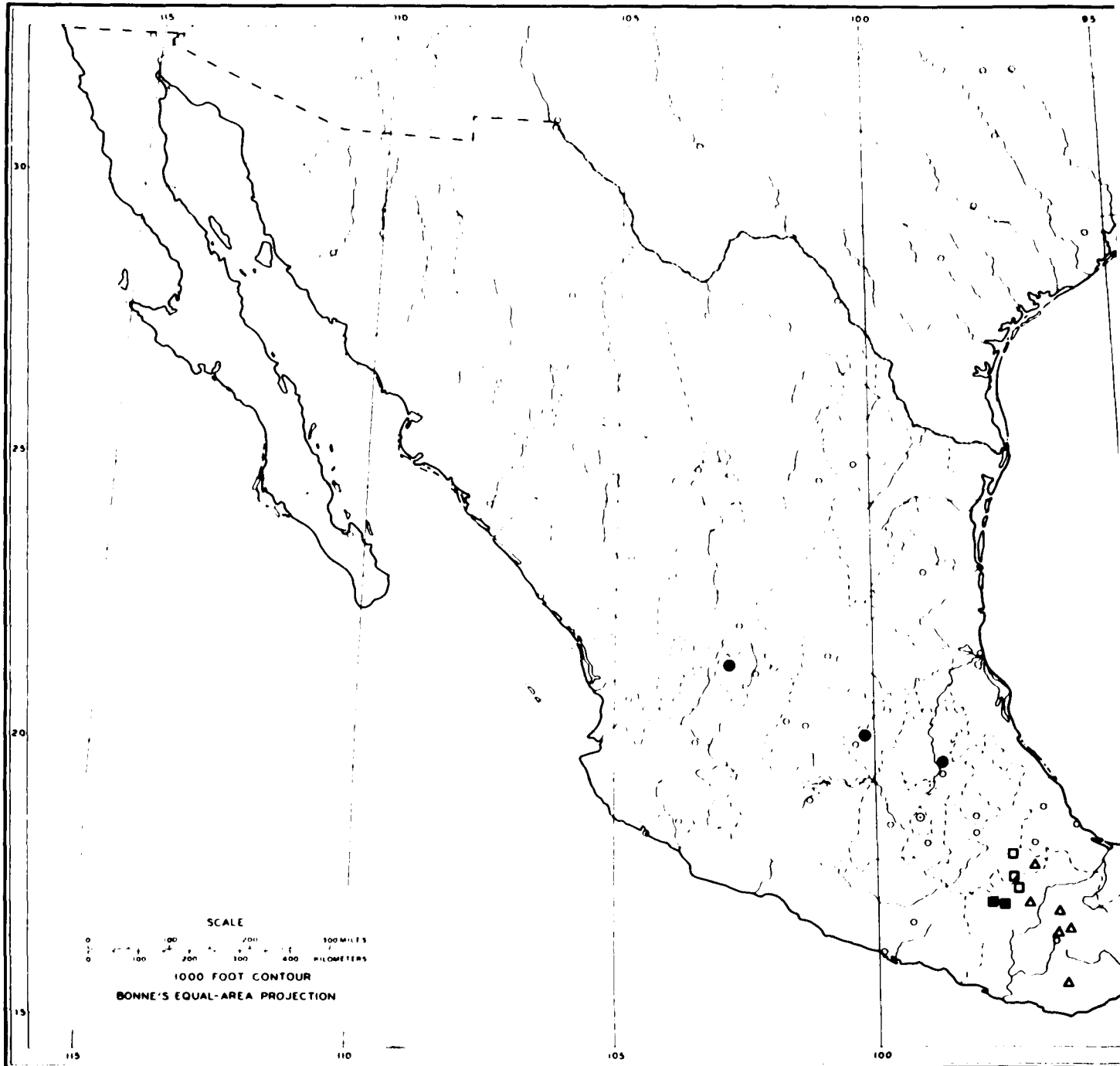


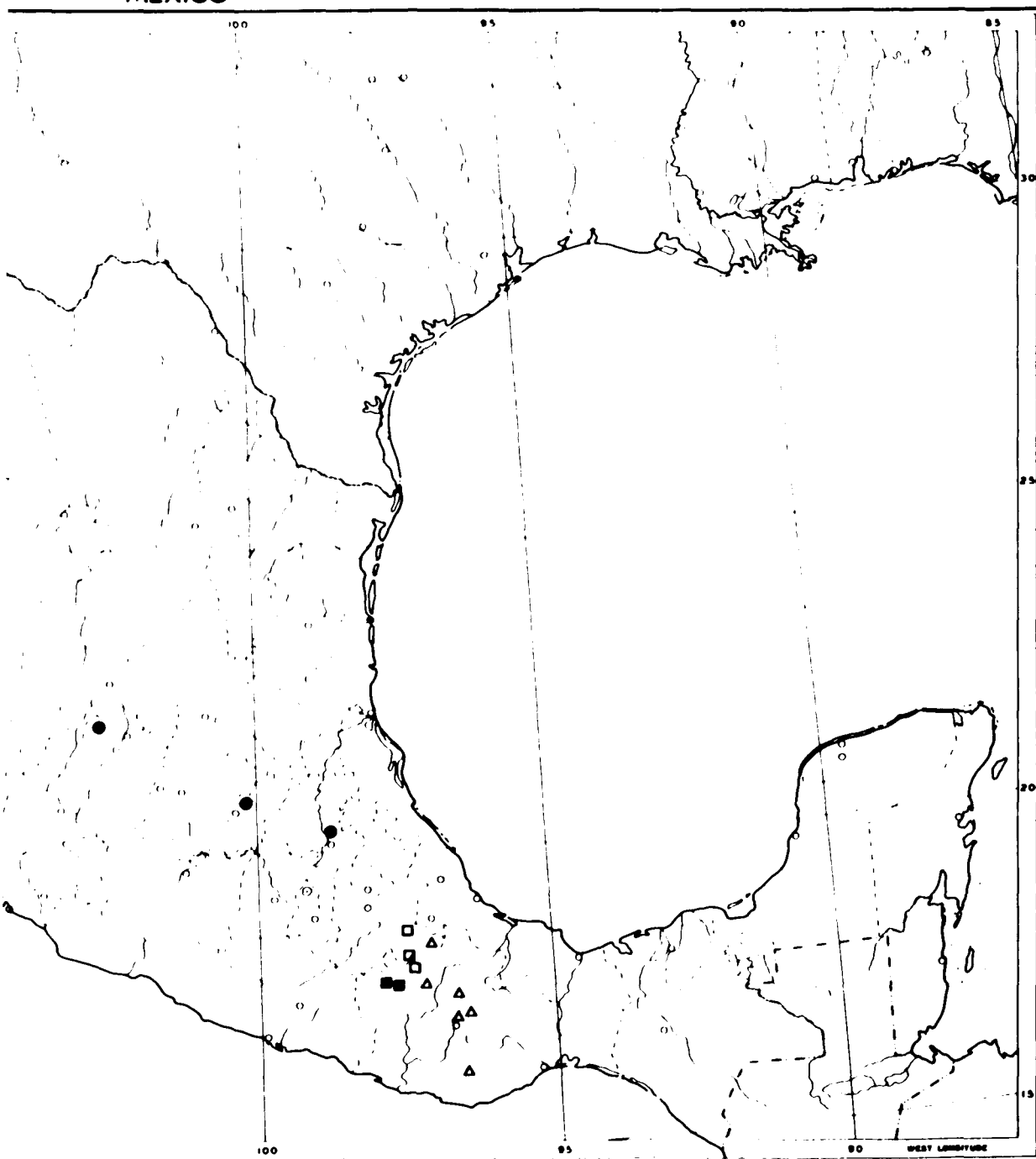
Figure 41. Schoenocaulon macrocarpum. A, mature flower shown with unopened anthers, x 8; B, three tepals, x 9.5; C, cross-section of mature capsule, x 4.8; D, long-section of mature flower, x 8; E, immature capsule, x 4; F, seeds, x 8 (A-B & D, Frame 393; C & E-F, Frame 390).

Map 1. Distribution of Schoenocaulon caricifolium [var. caricifolium (●), var. oaxacense (■)], Schoenocaulon tenorioi (□), and Schoenocaulon tenuifolium (Δ).

MEXICO

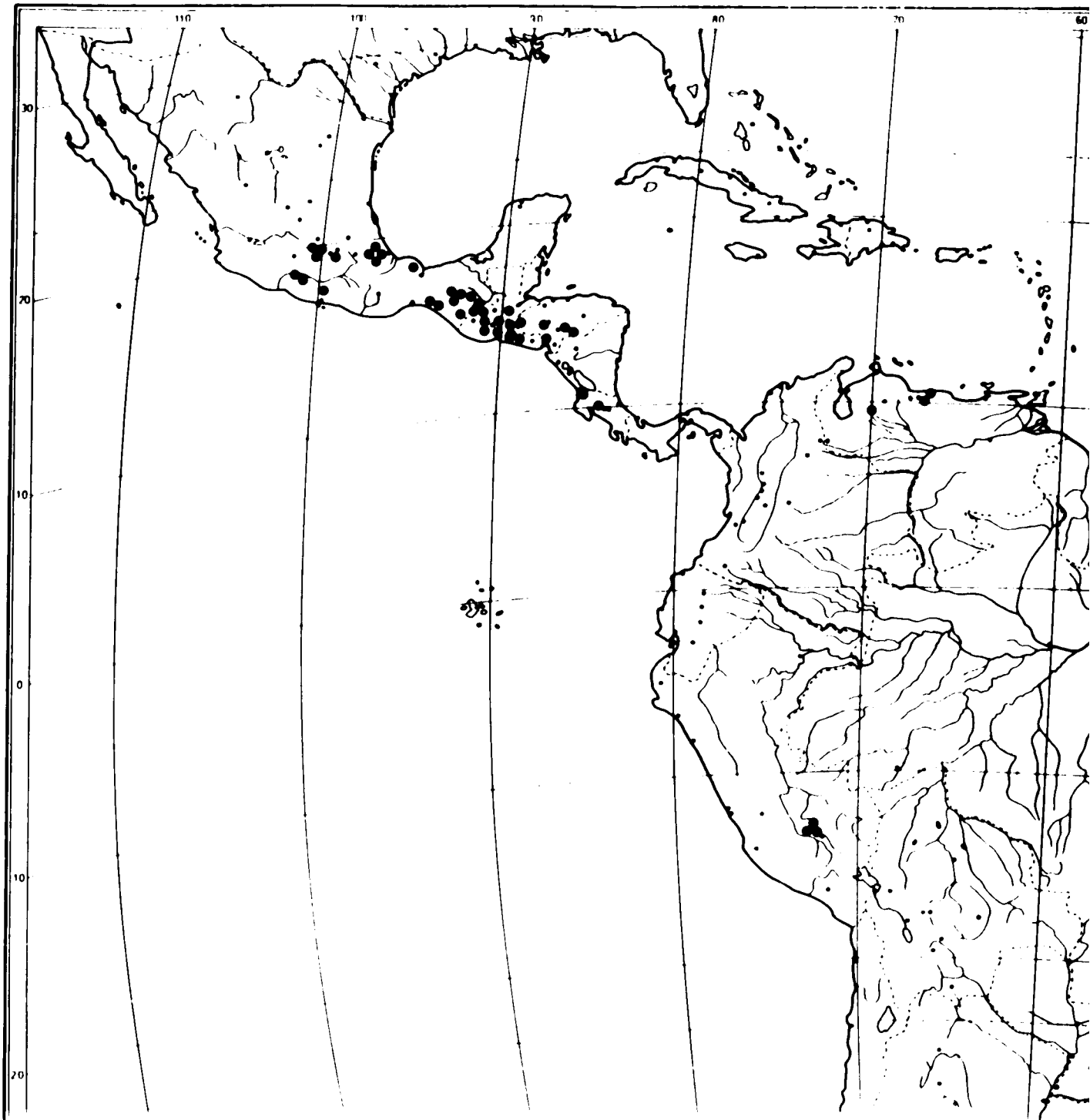


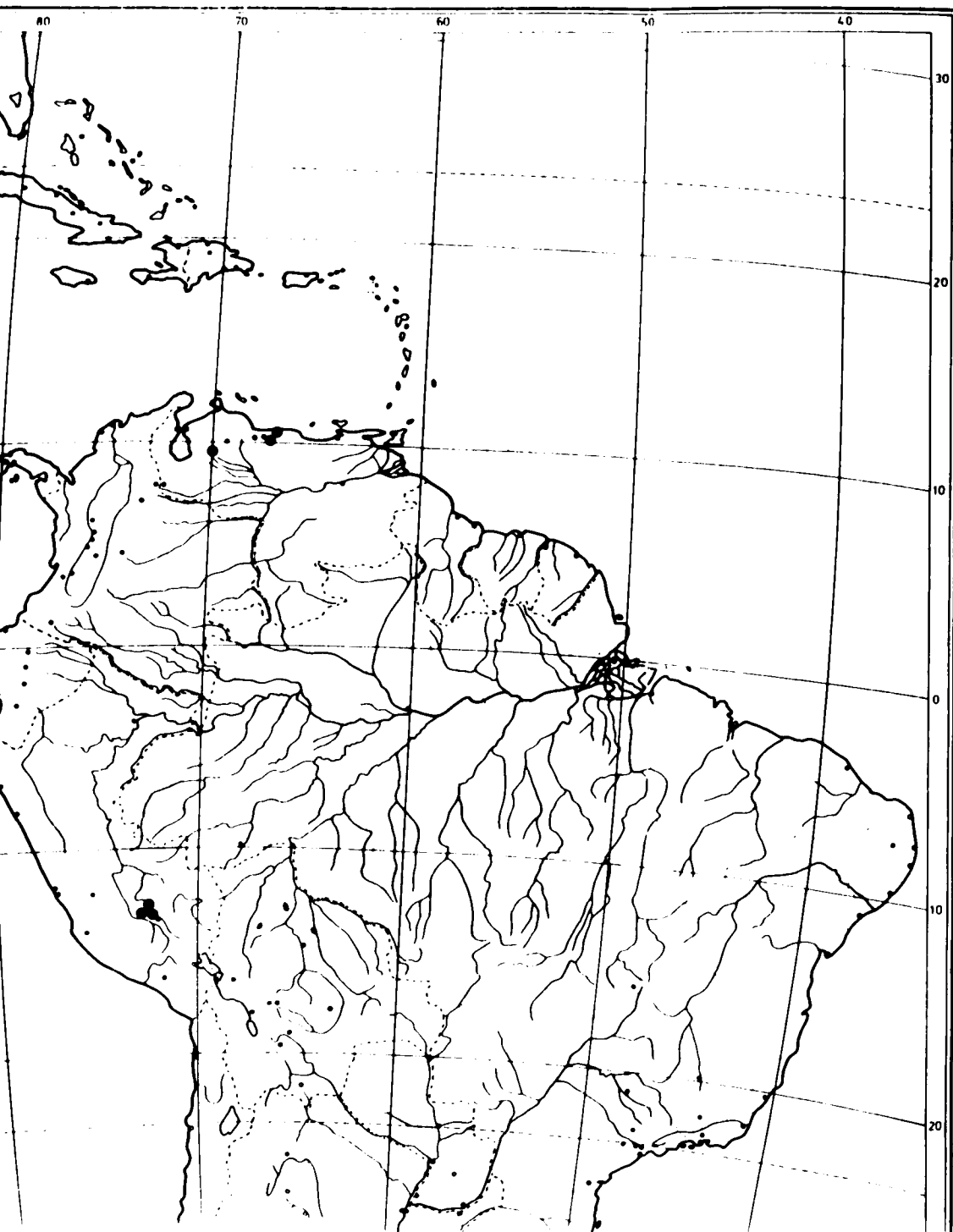
MEXICO



Map 2. Distribution of Schoenocaulon officinale (●).

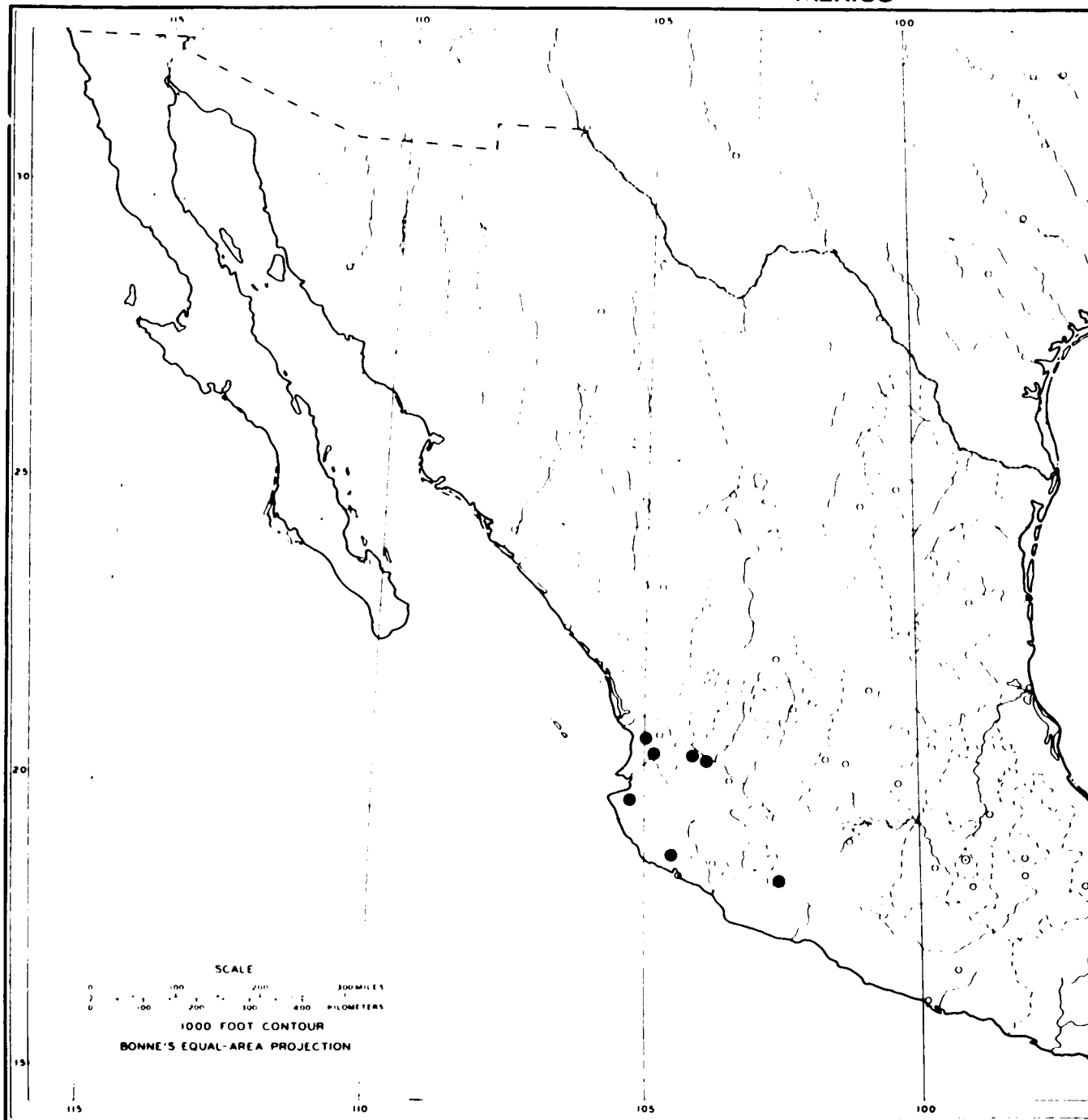
TROPICAL AMERICA



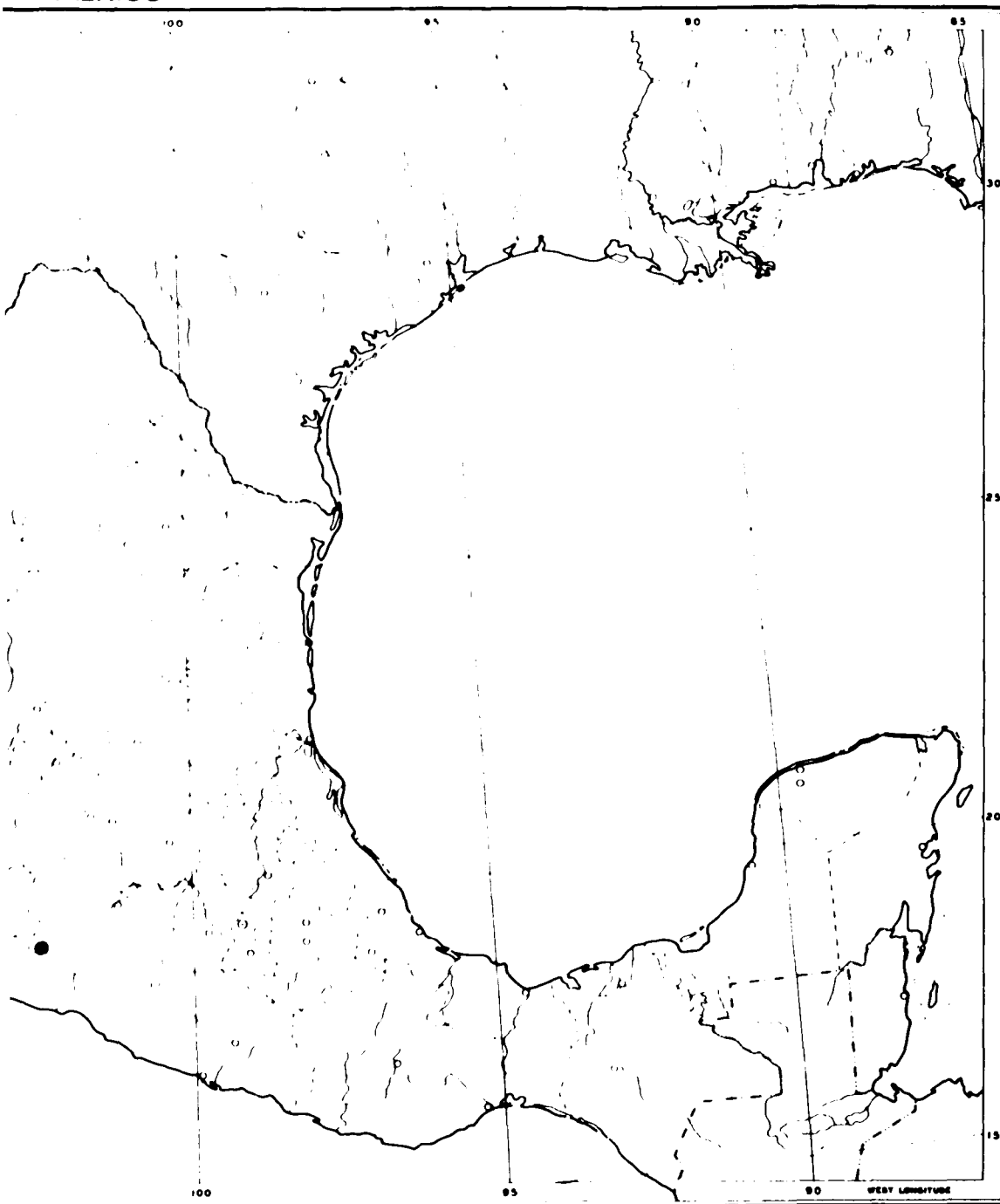


Map 3. Distribution of Schoenocaulon pellucidum (●).

MEXICO

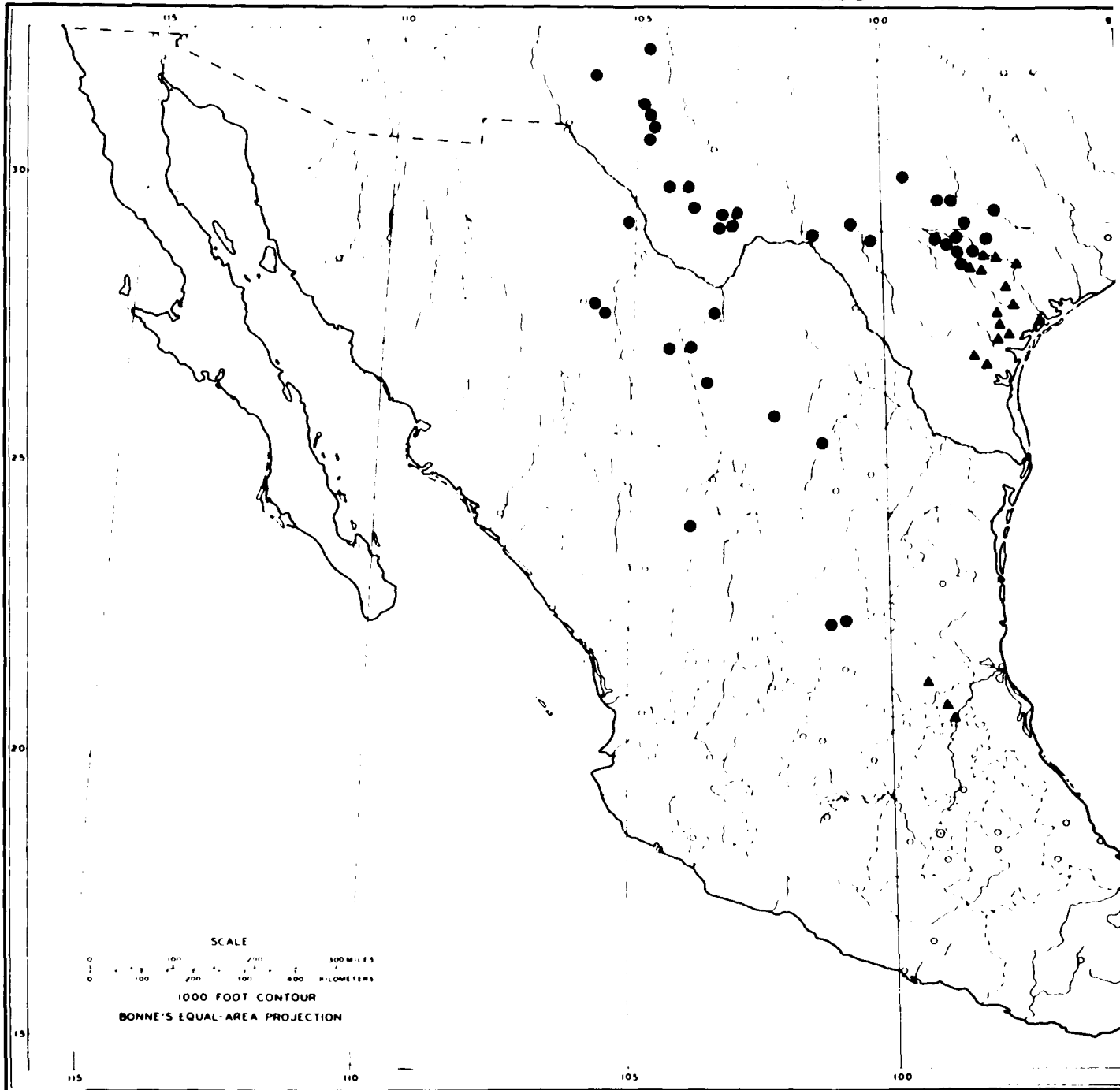


MEXICO

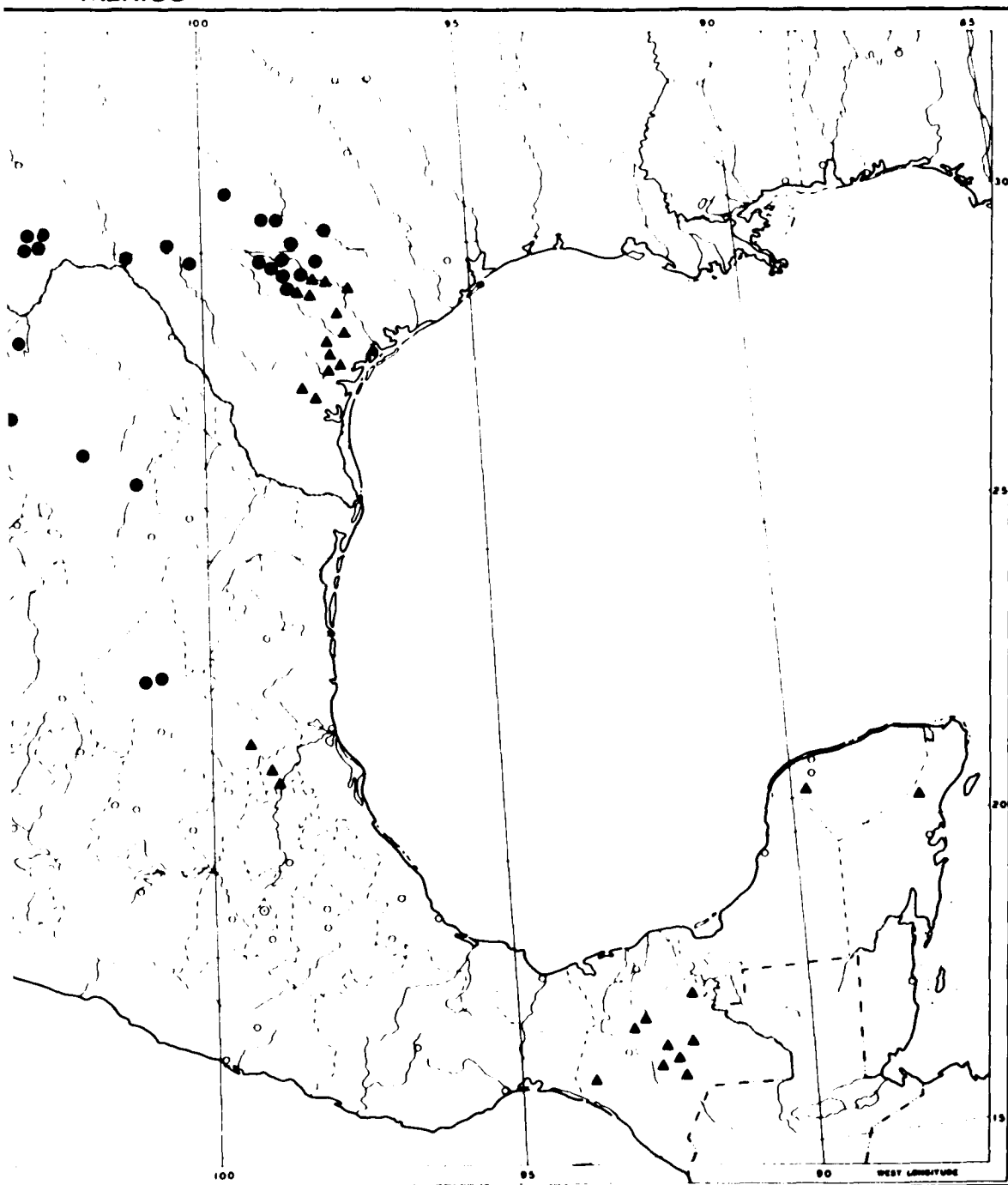


Map 4. Distribution of Schoenocaulon ghiesbreghtii (▲), and Schoenocaulon texanum (●).

MEXICO

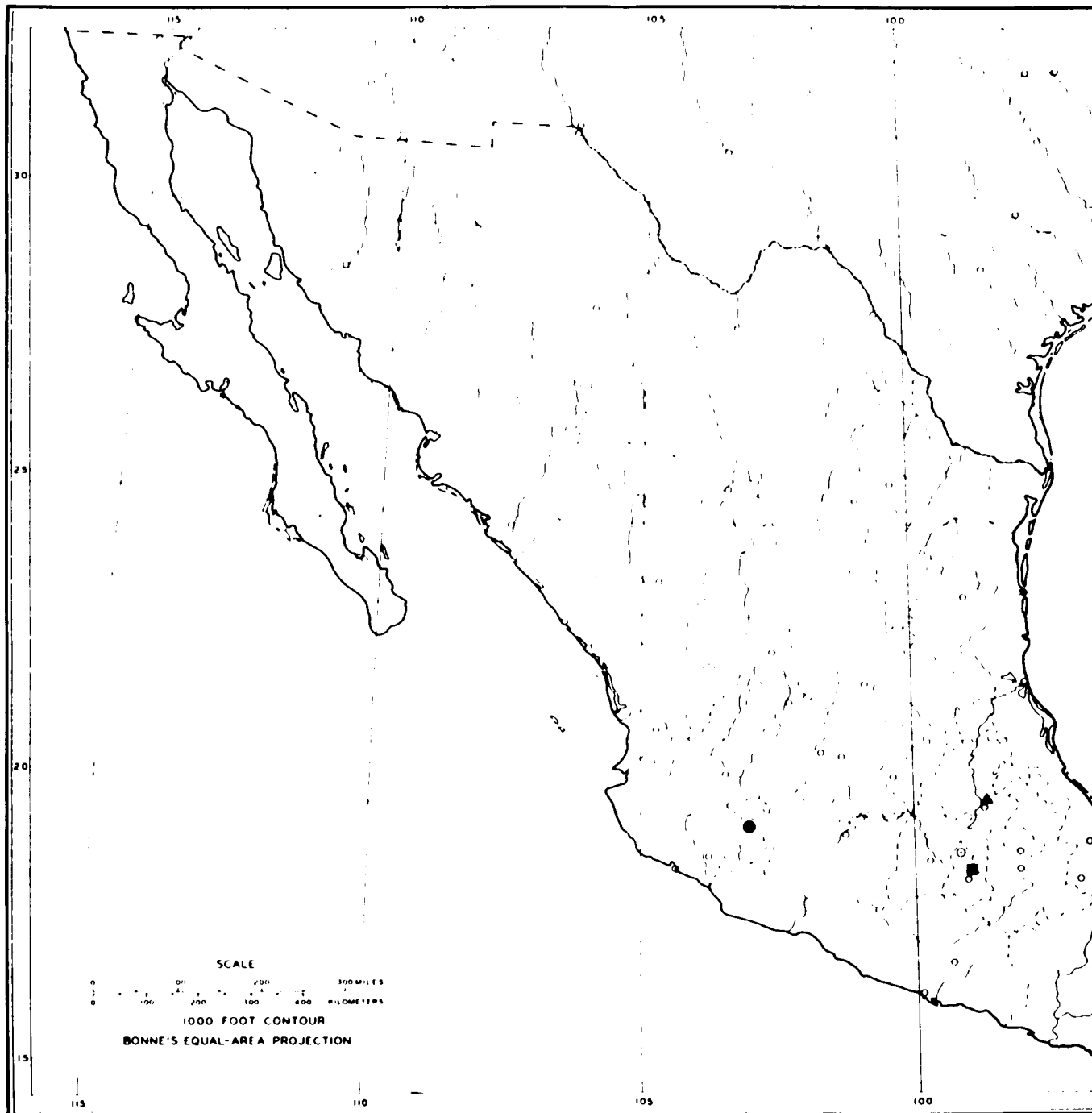


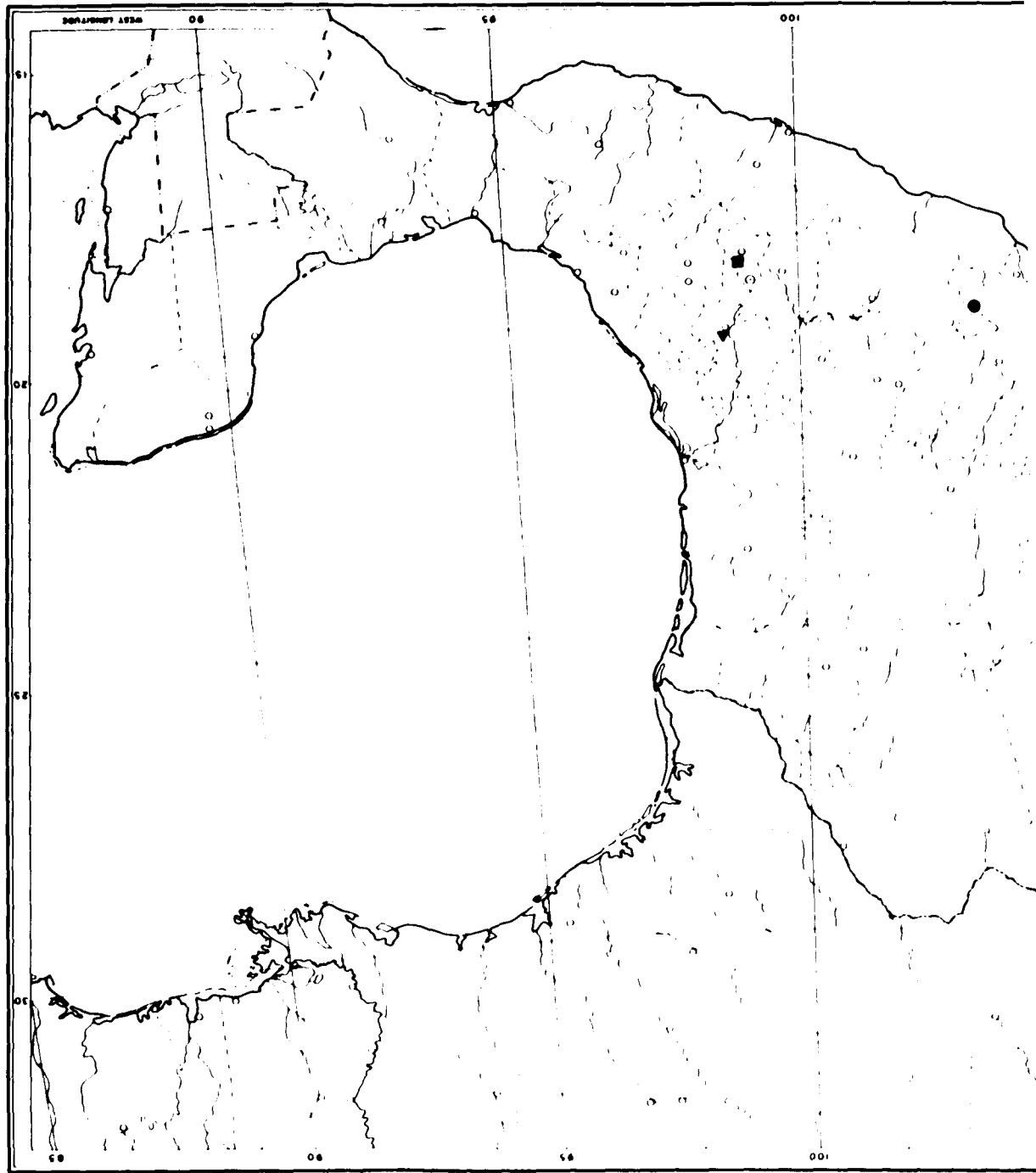
MEXICO



Map 5. Distribution of Schoenocaulon tigrense (●), Schoenocaulon obtusum (▲), and Schoenocaulon tenue (■).

MEXICO

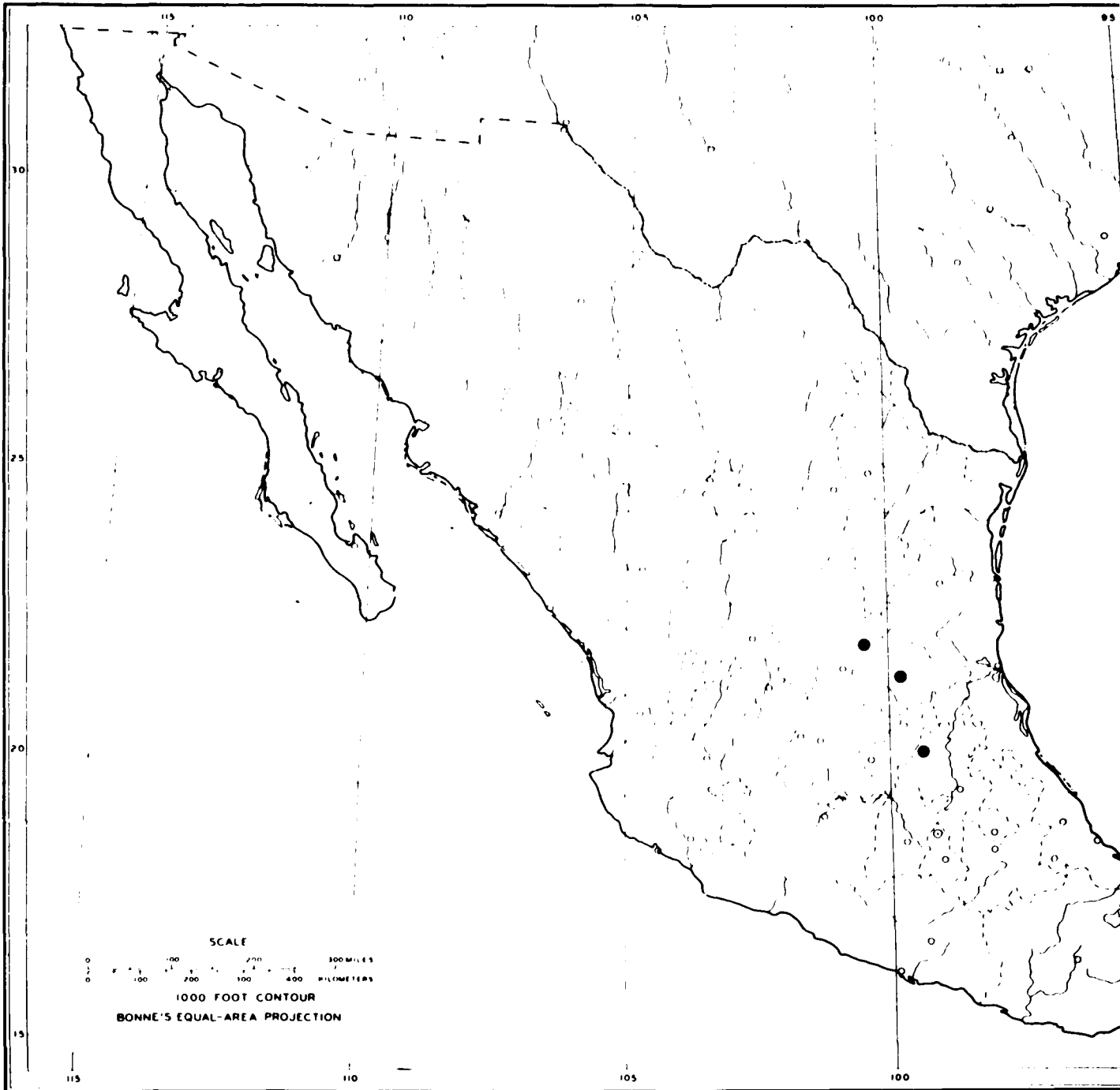


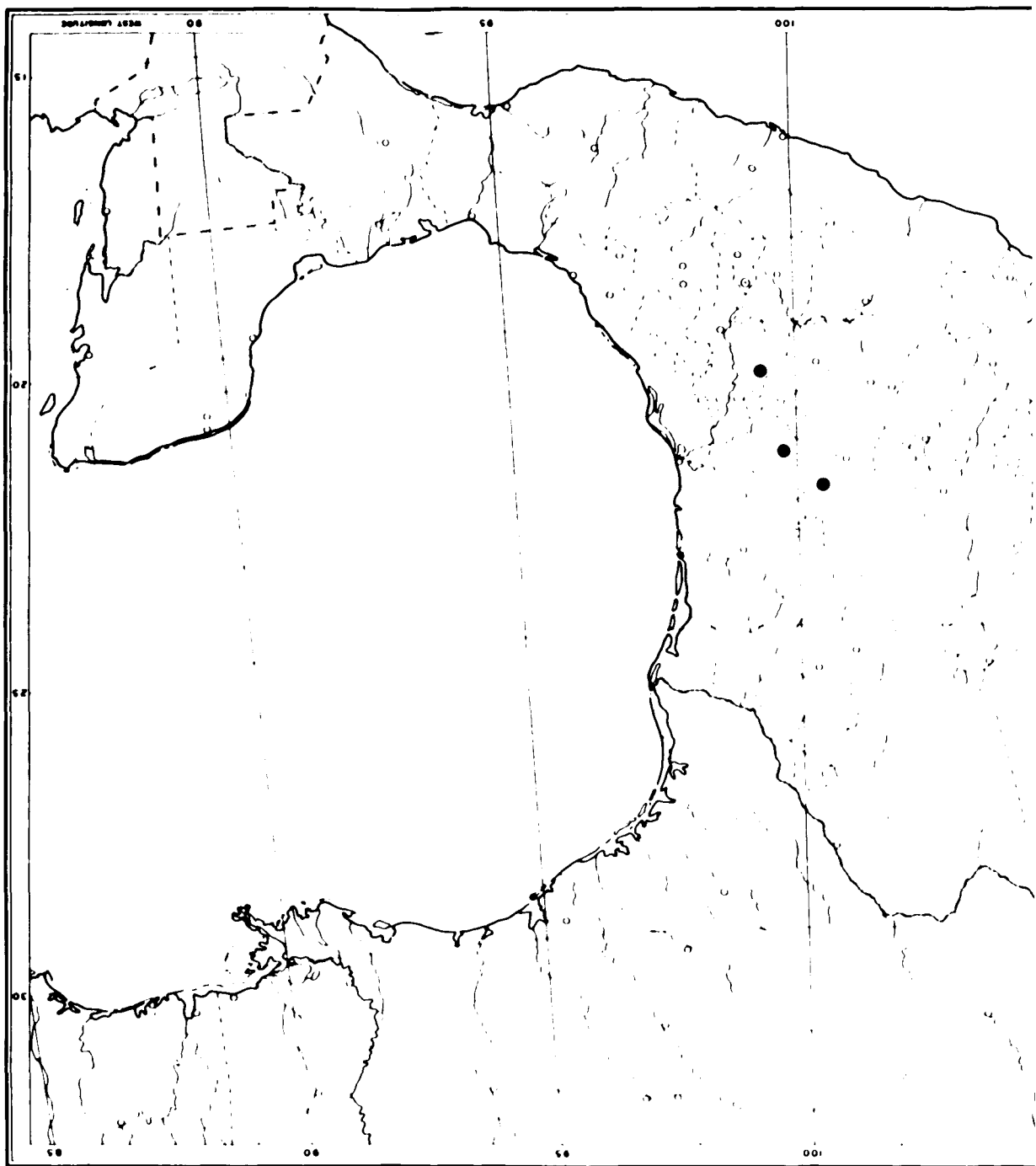


MEXICO

Map 6. Distribution of Schoenocaulon intermedium (●).

MEXICO

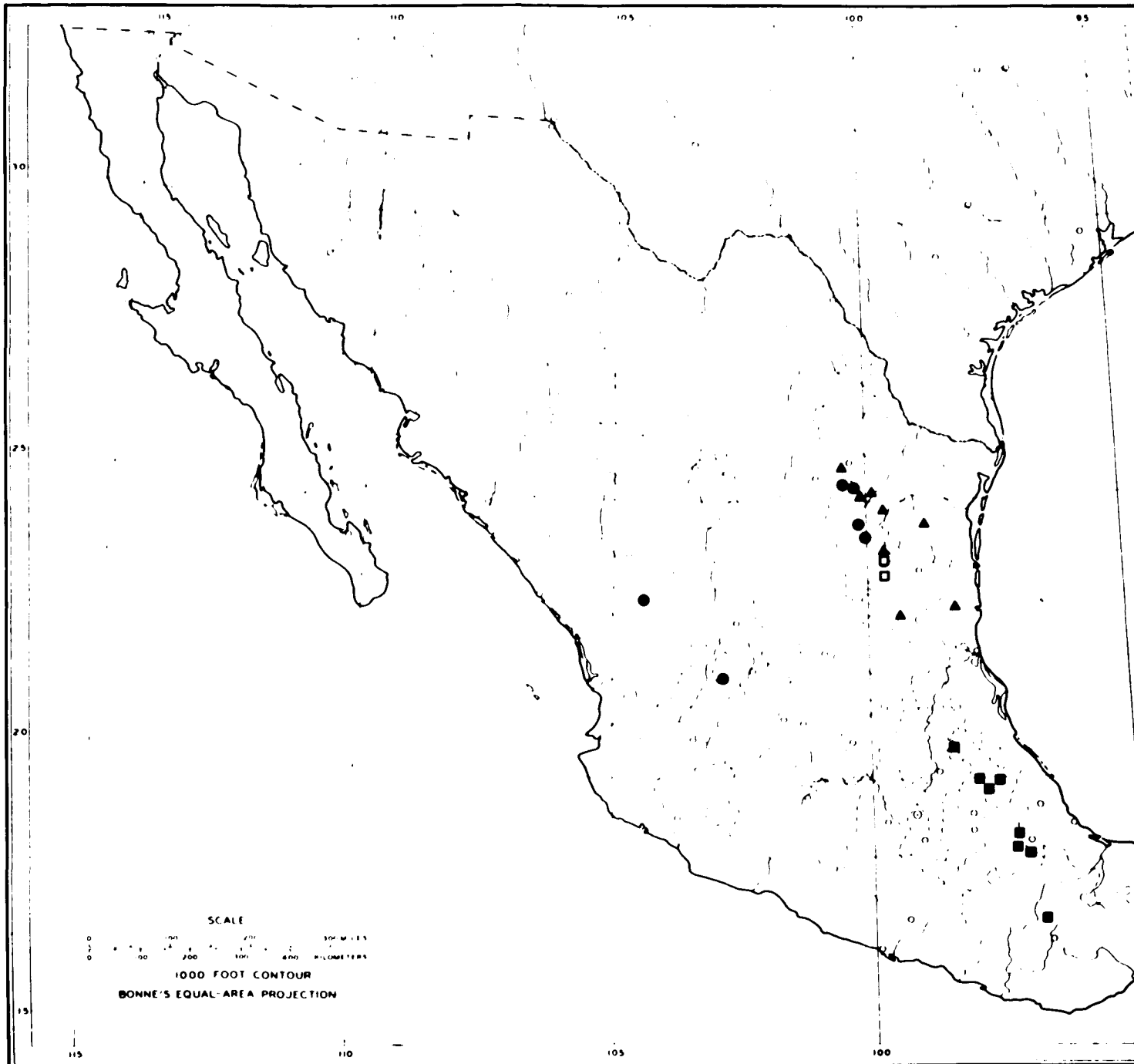


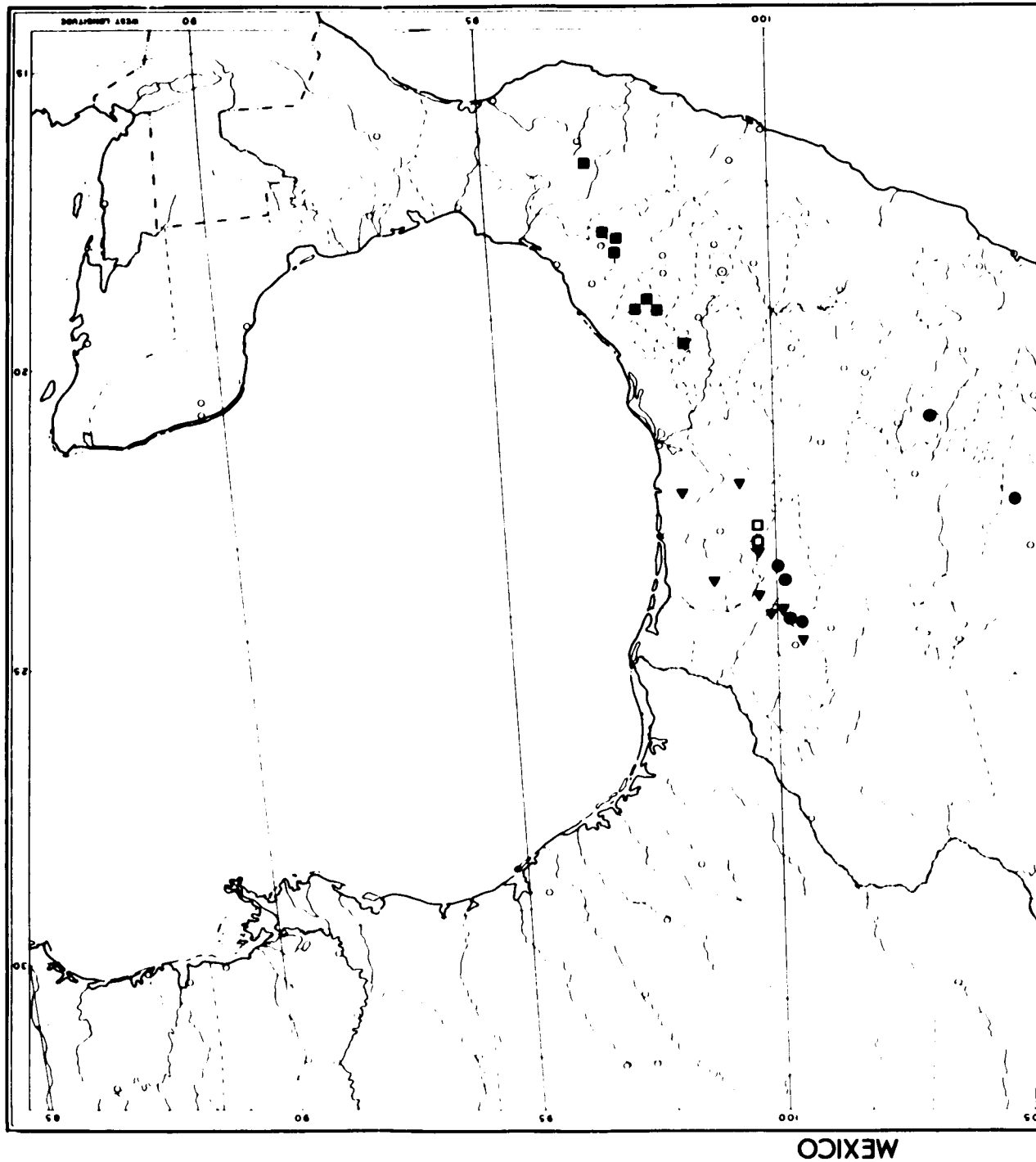


MEXICO

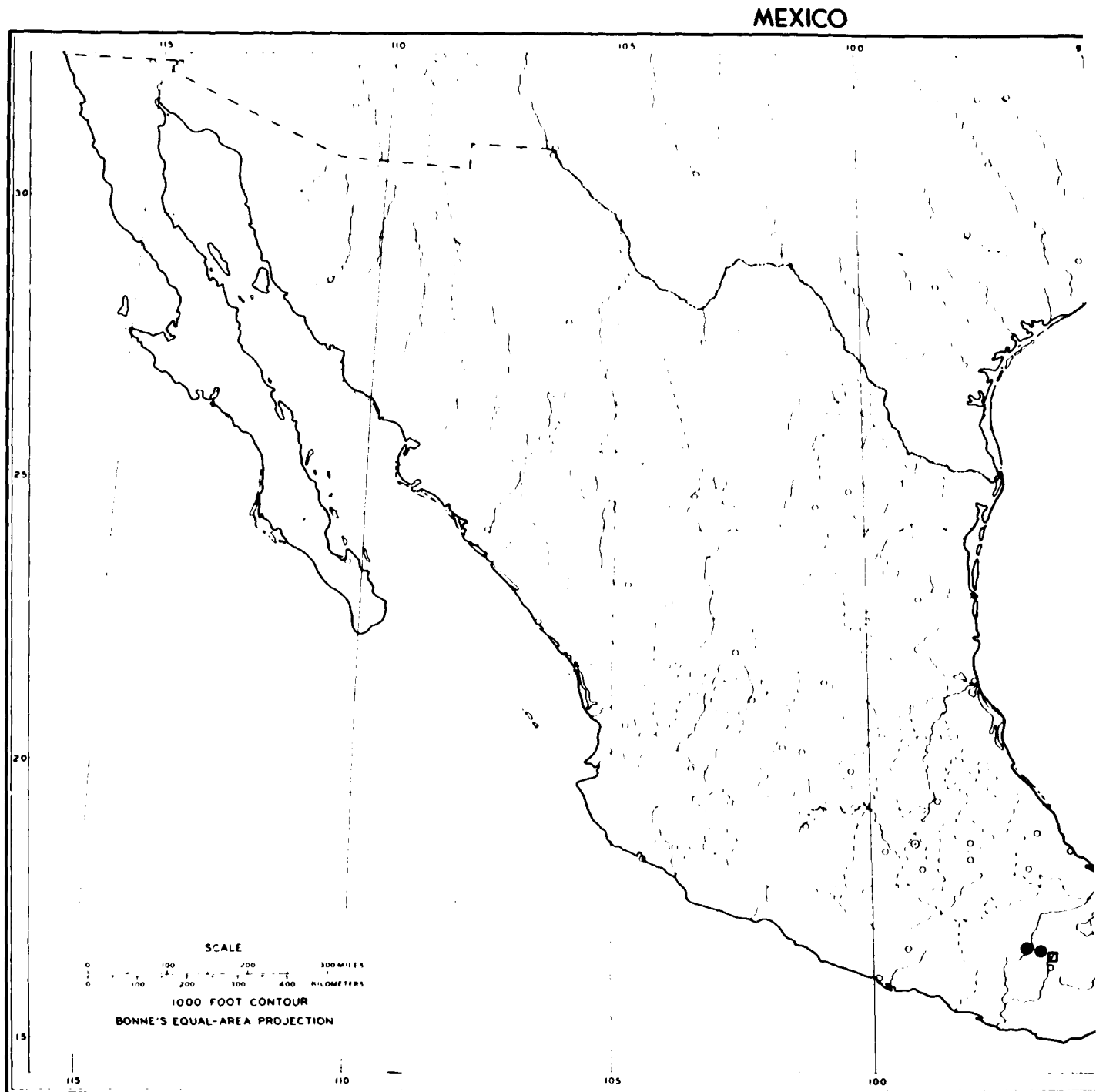
Map 7. Distribution of Schoenocaulon ignigenum (□), Schoenocaulon macrocarpum (●), Schoenocaulon madidorum (■), and Schoenocaulon plumosum (▲).

MEXICO

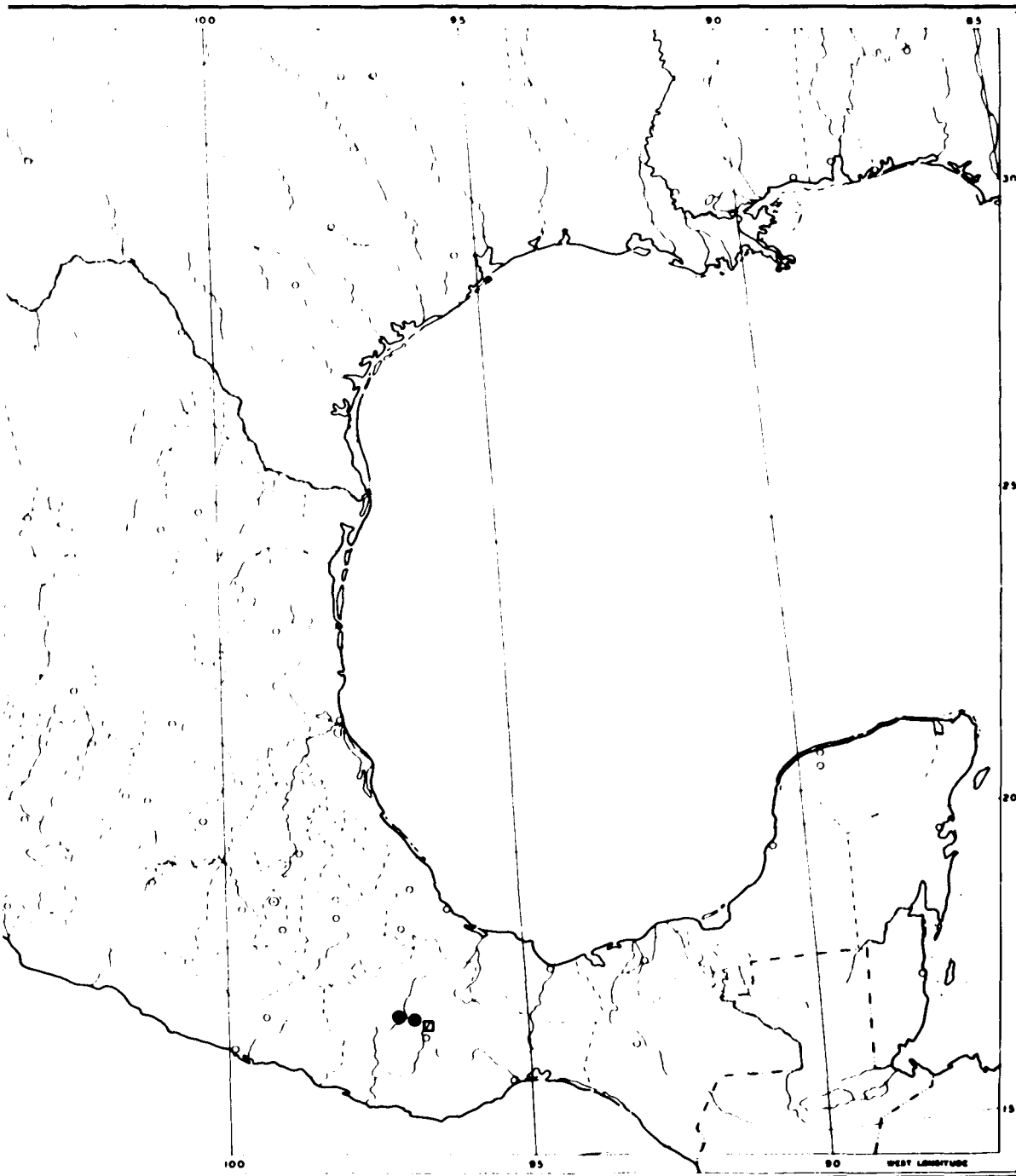




Map 8. Distribution of Schoenocaulon calcicola (●), and Schoenocaulon conzattii (□).

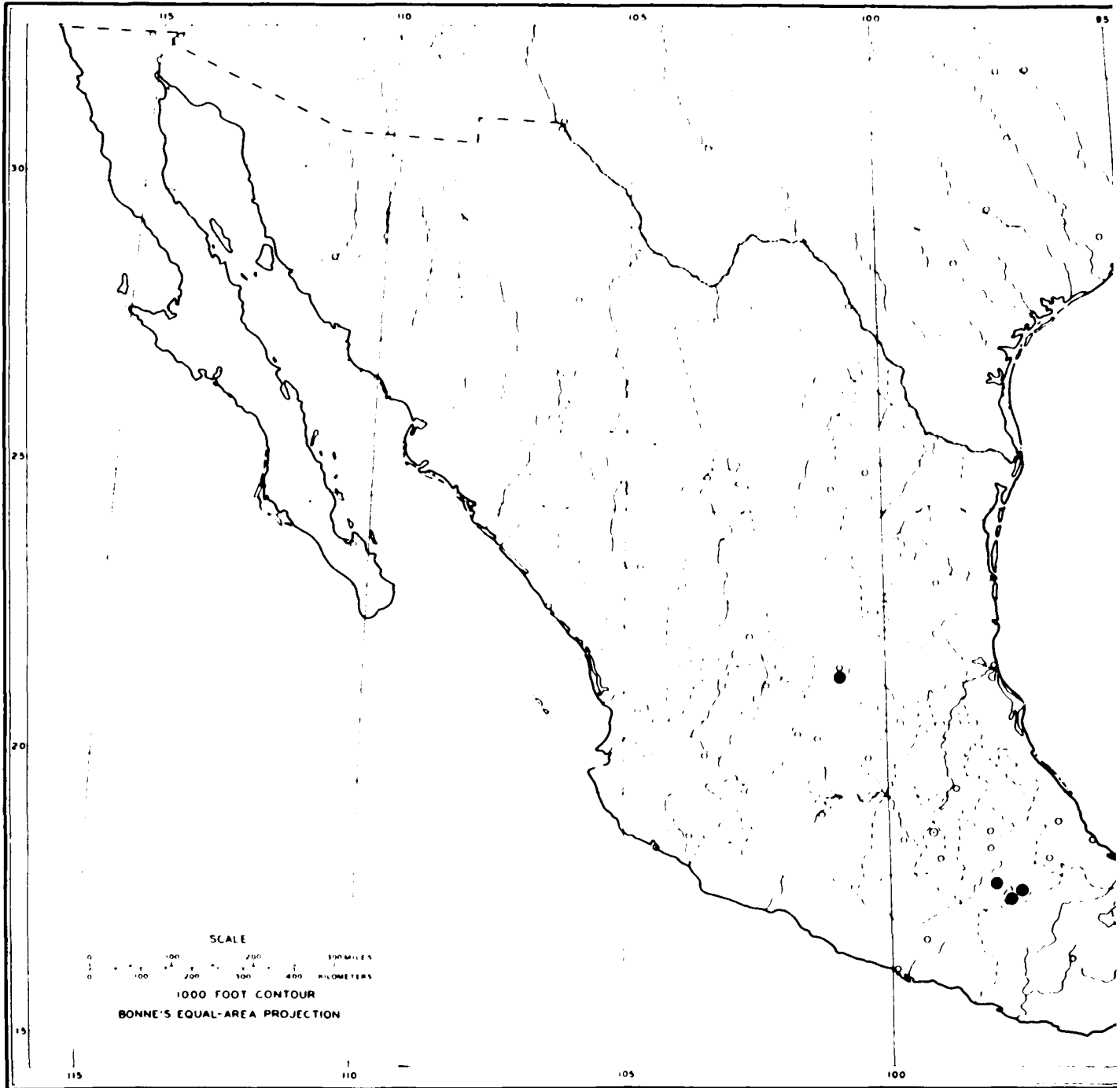


MEXICO

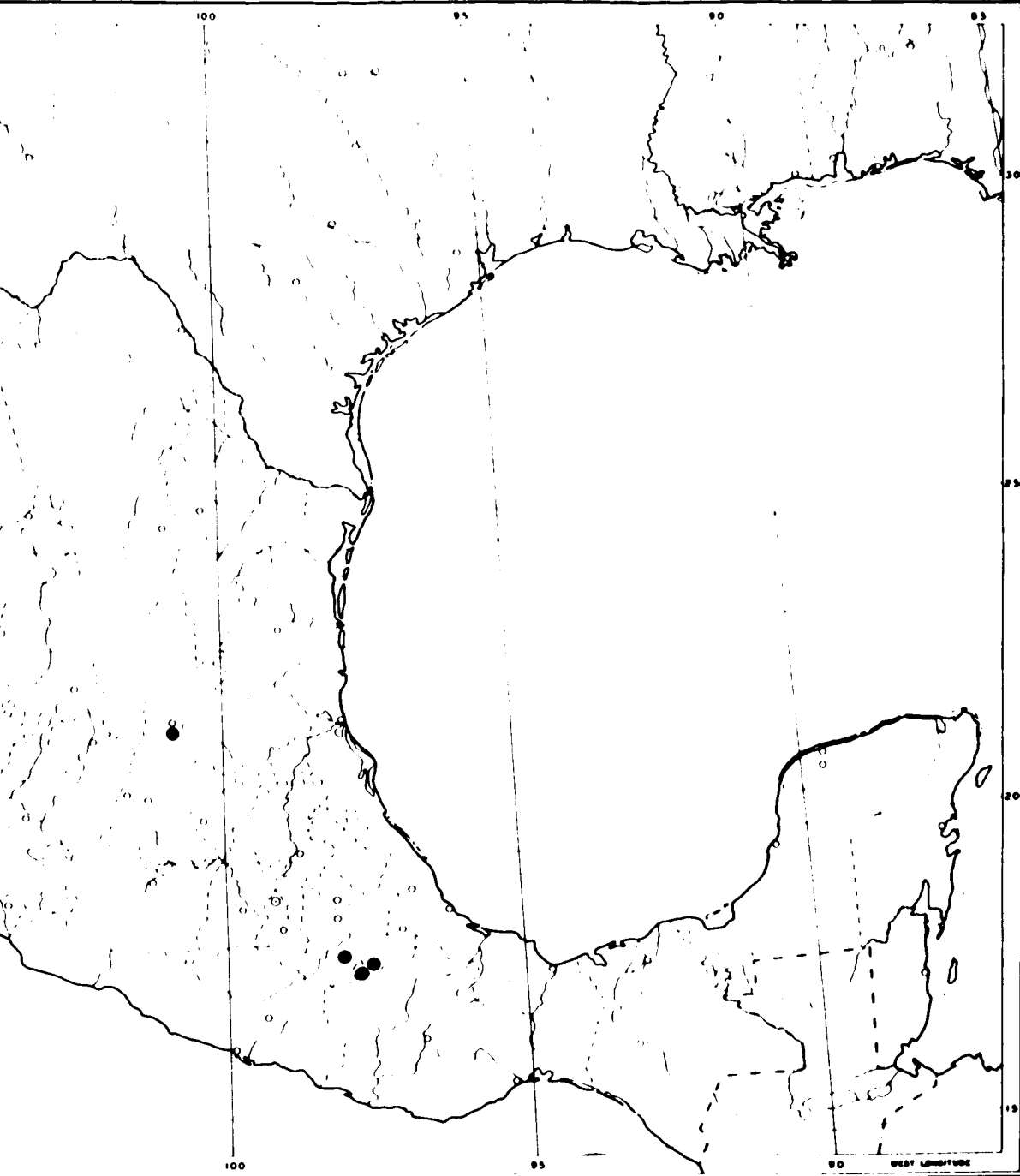


Map 9. Distribution of Schoenocaulon comatum (●).

MEXICO

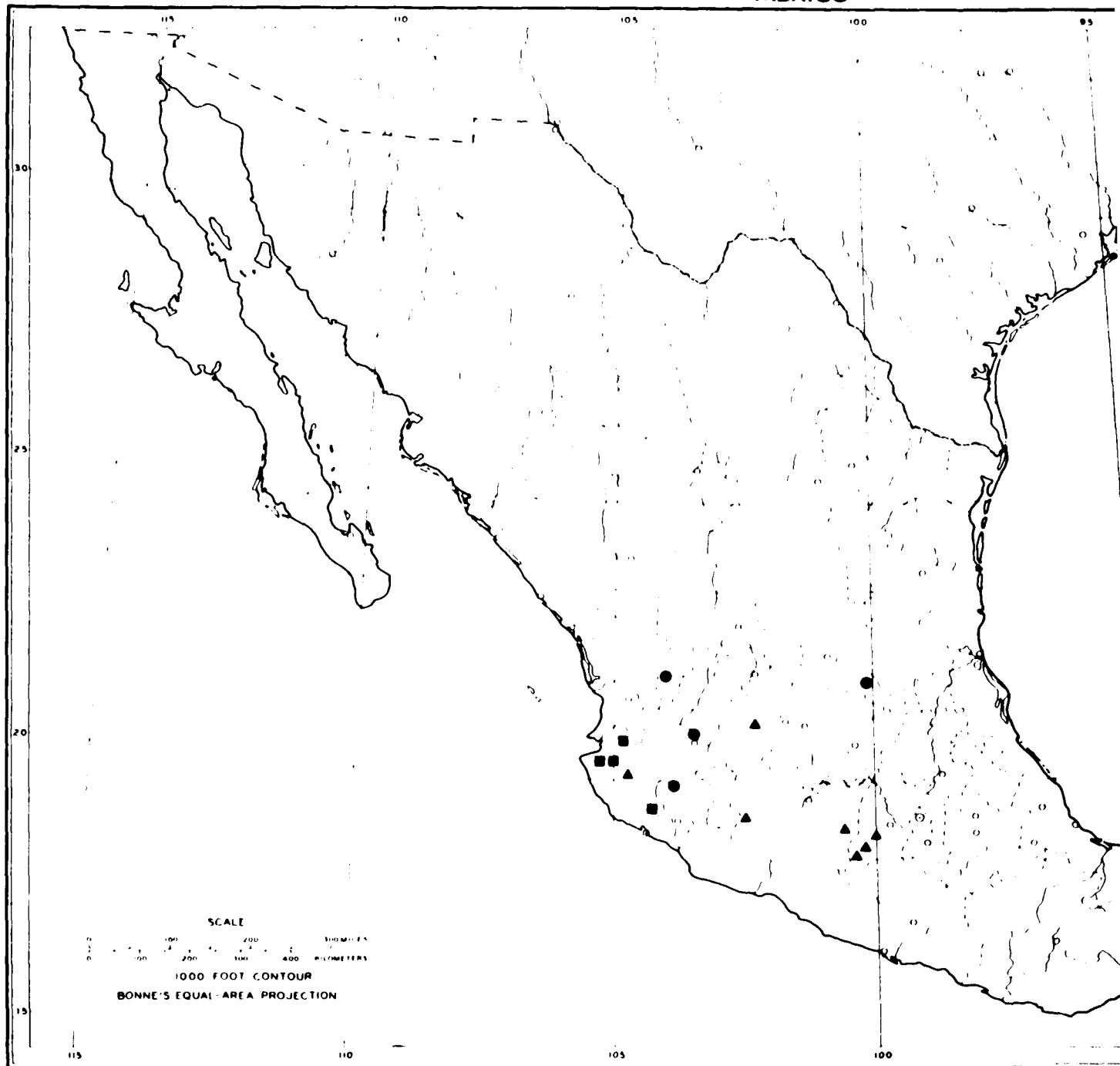


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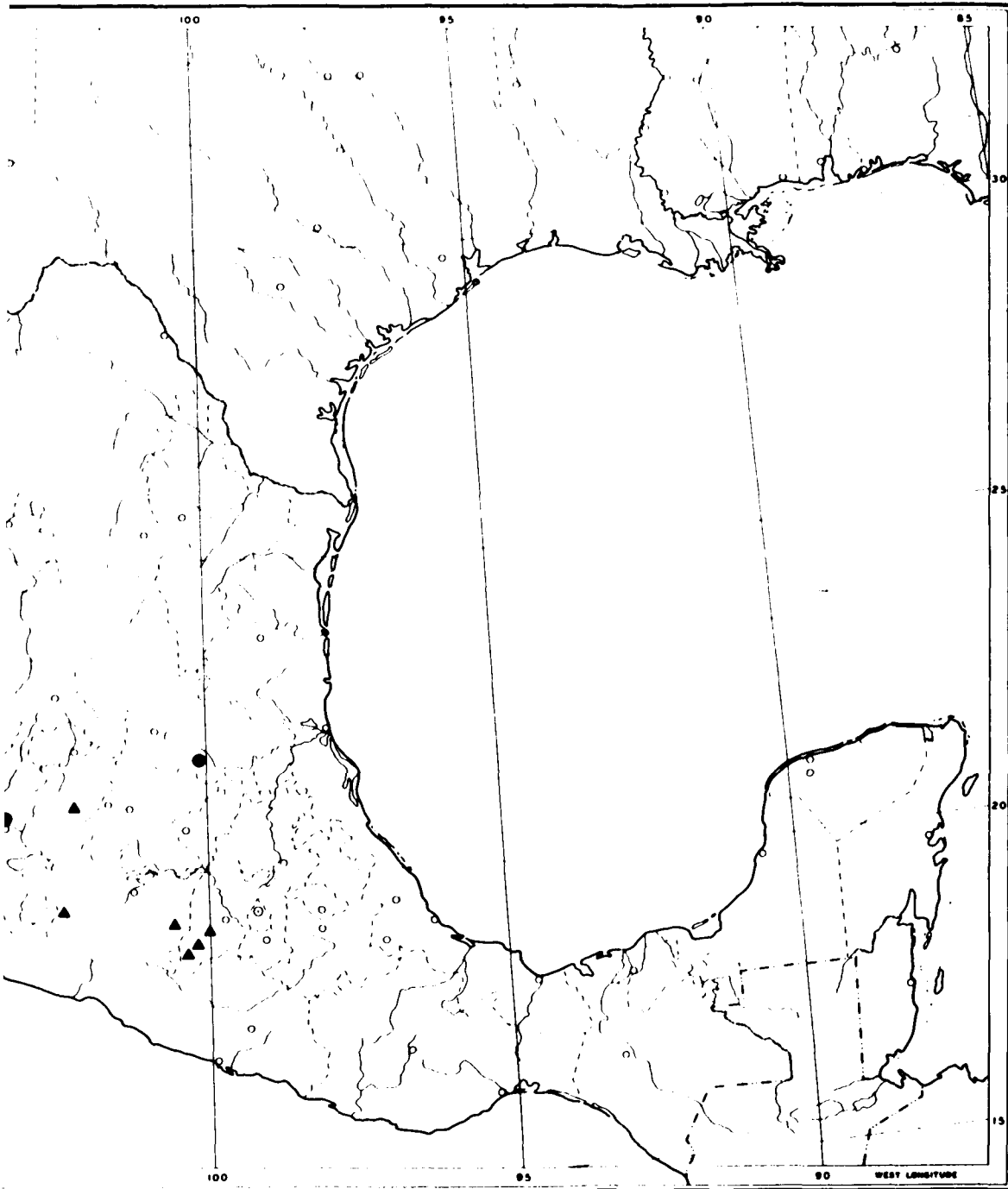


Map 10. Distribution of Schoenocaulon jaliscense [var. jaliscense (●), var. regulare (■)], and Schoenocaulon mortonii (▲).

MEXICO



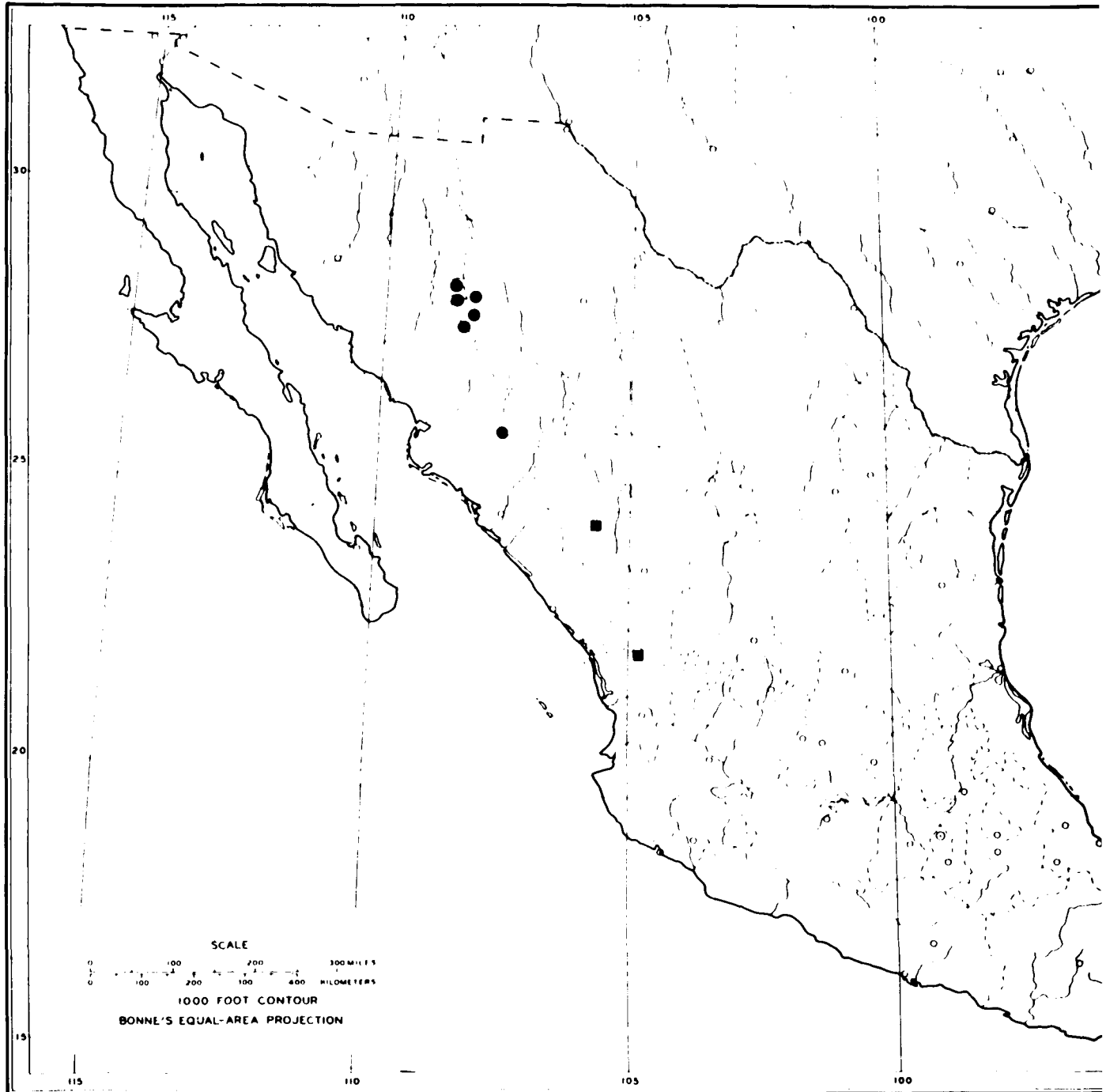
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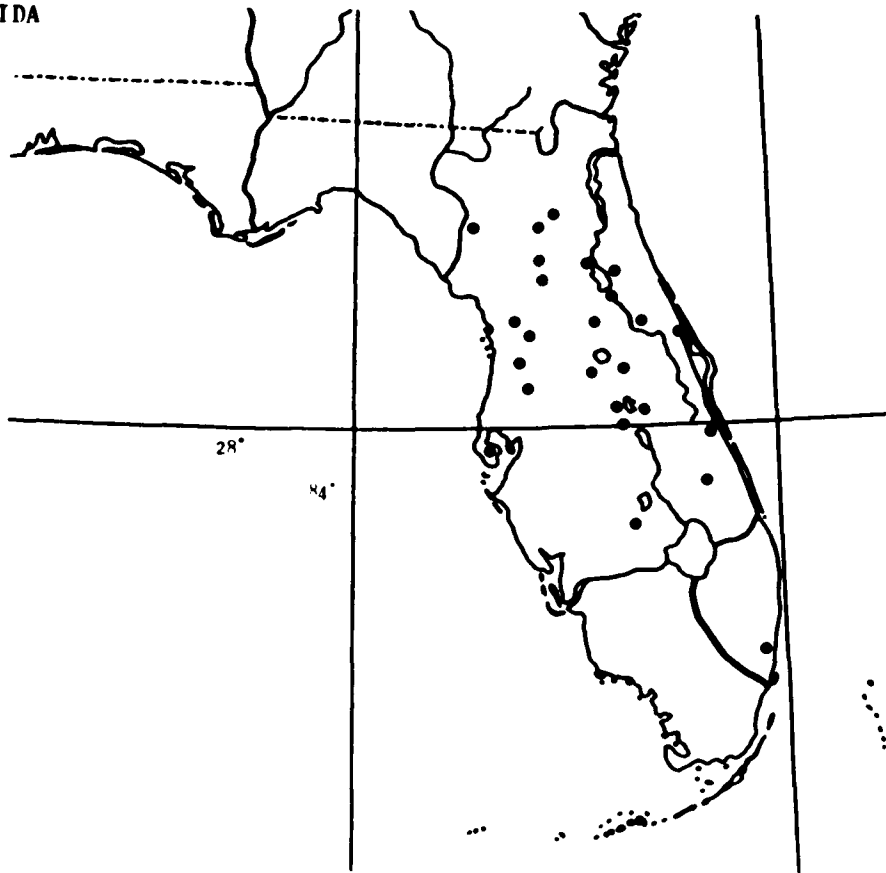
Map 11. Distribution of Schoenocaulon megarrhizum [var. megarrhizum (●), var. deminutum (■)].

MEXICO



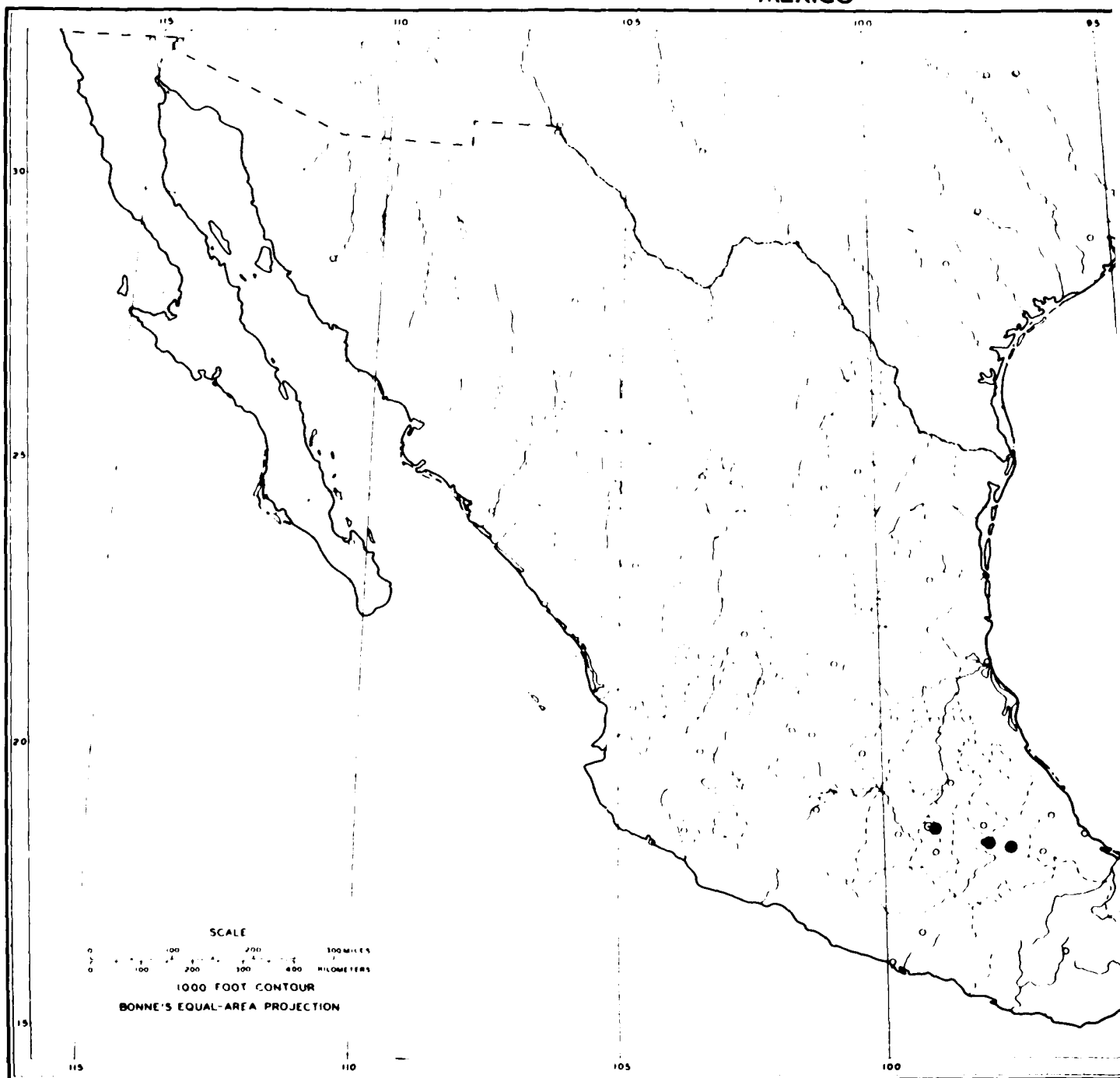
Map 12. Distribution of Schoenocaulon dubium (●).

FLORIDA

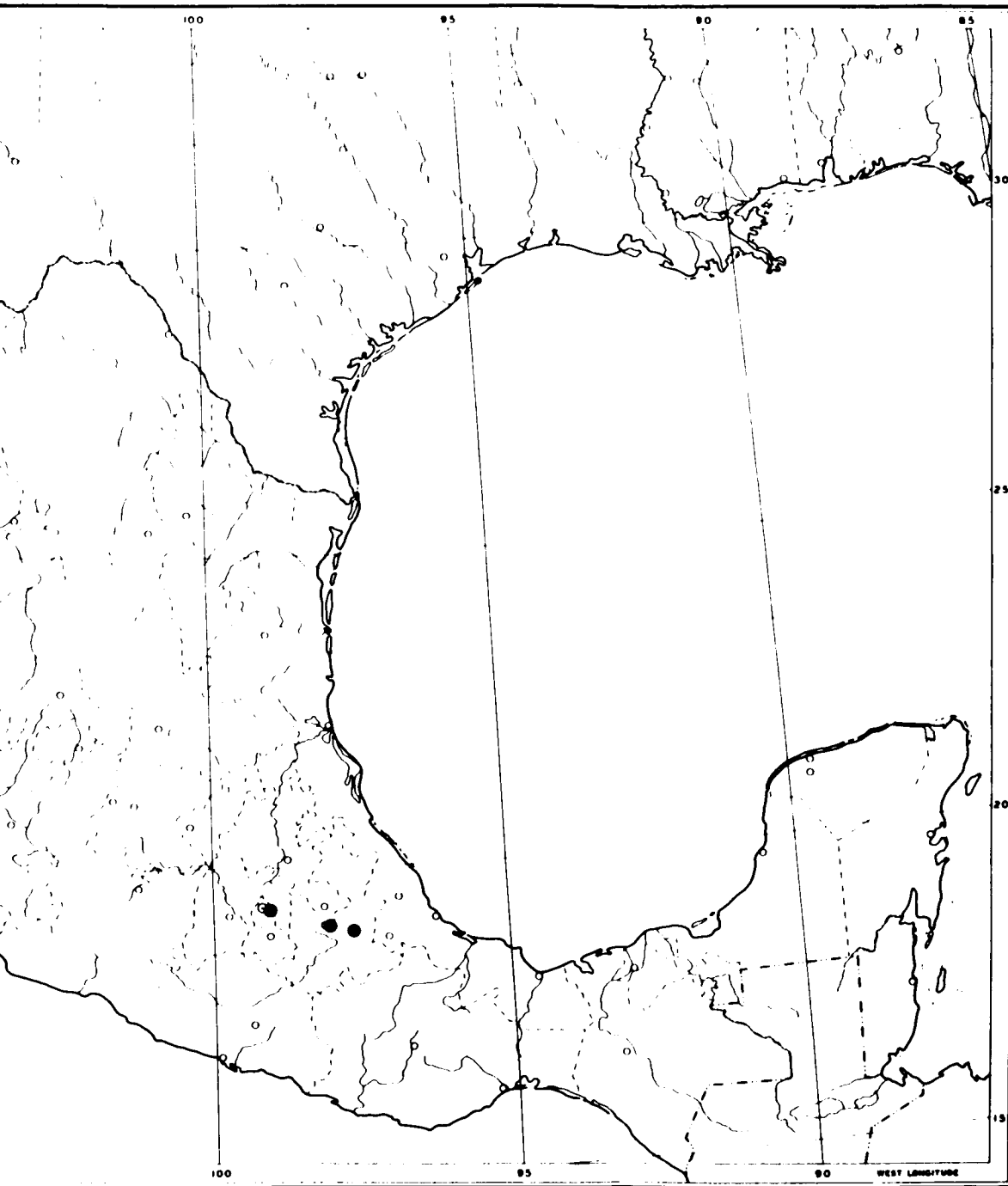


Map 13. Distribution of Schoenocaulon rzedowskii (●).

MEXICO

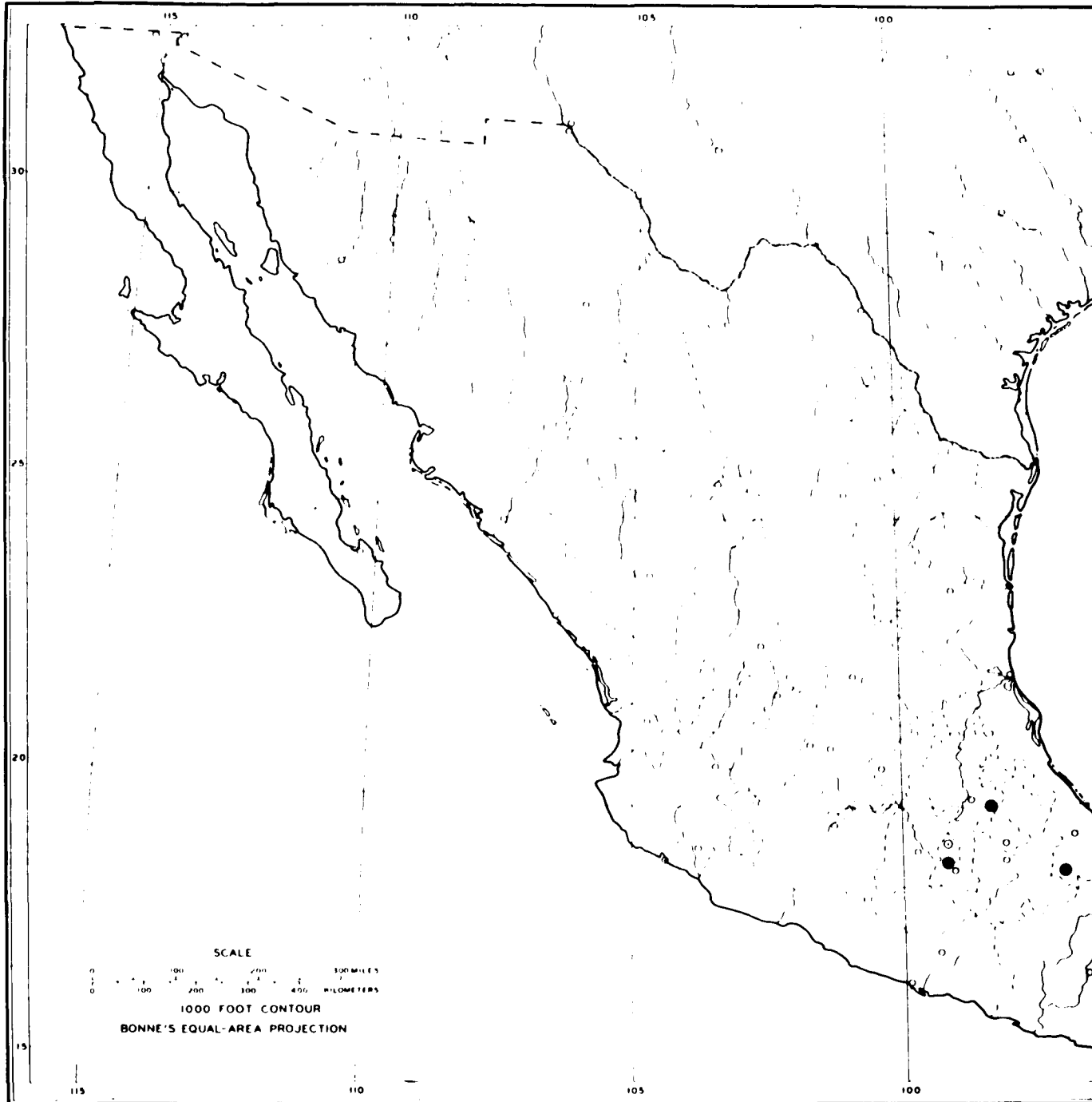


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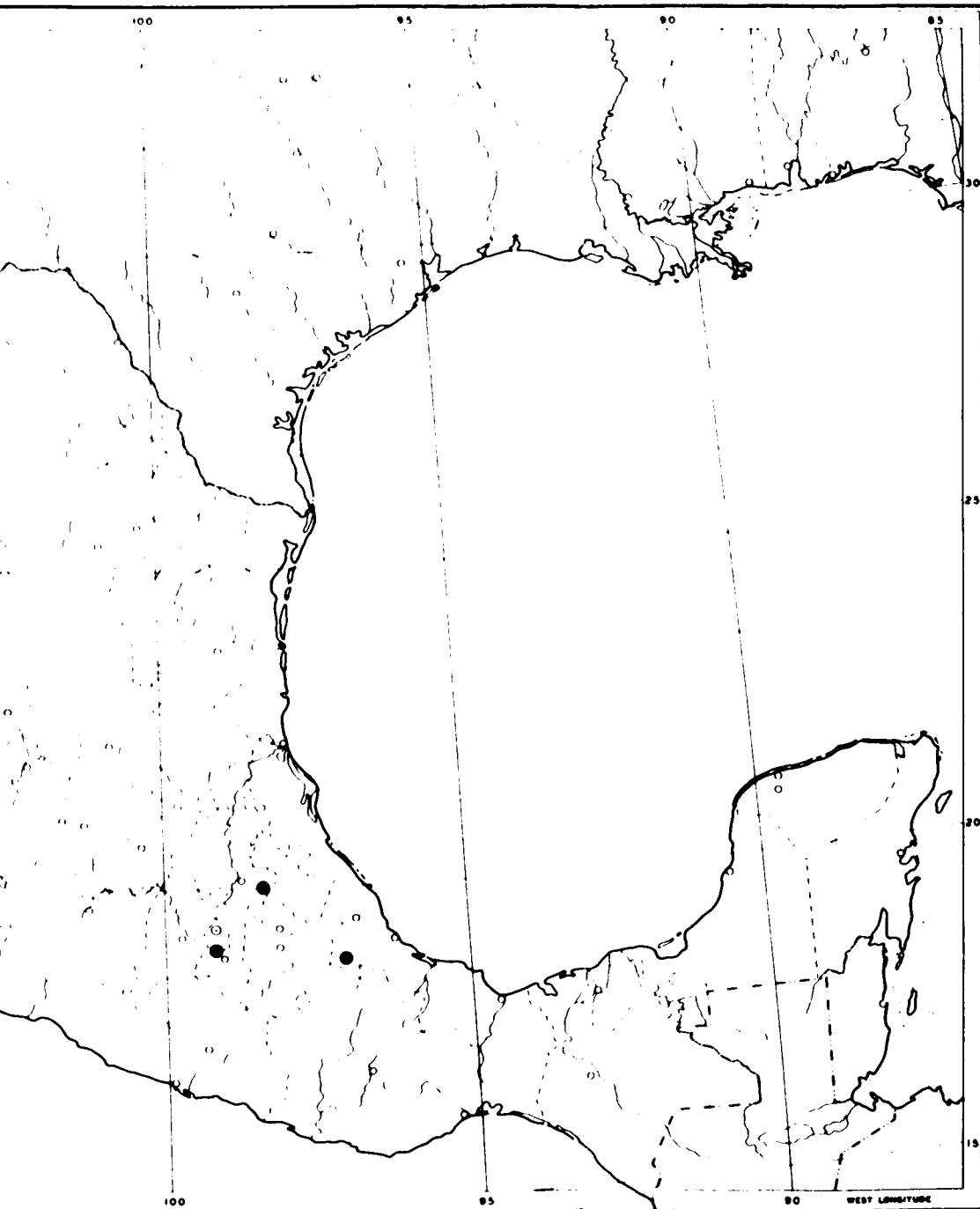


Map 14. Distribution of Schoenocaulon pringlei (●).

MEXICO



MEXICO



Chapter VII: Evolution

The characters that differentiate species in Schoenocaulon are usually subtle. For this reason, it is difficult to interpret the precise pattern of evolution within the genus. A few species are strikingly different and clearly advanced, such as S. tenuifolium, with red, campanulate in outline flowers; S. officinale with specialized nectary pads; S. ghiesbreghtii with long filaments and denticulate tepal margins; and S. pellucidum with mostly cream-colored tepals of petaloid texture. However, the majority of species seem to be distinguished by various combinations of relatively few characters. As the features defining most species cannot be confidently held to be unidirectional in their evolutionary progression, a satisfactory phylogeny of the genus is not possible at present. A discussion of the affinities of species may be found in the section of the the same name in the chapter entitled: taxonomic treatment.

It is of course arguable that if the differences between Schoenocaulon species are so subtle, they may be biologically insignificant. There are two obstacles to this hypothesis. First, most species of archaic monocot genera have fewer characters to distinguish them from each other than have those of archaic dicot genera, a fact doubtless related to their body plan, and by implication, to their evolutionary history. Second, the means by which Schoenocaulon is distributed. The seeds of Schoenocaulon are smooth and often fairly dense. The capsules merely dehisce along the sutures and the seeds fall to the earth in the immediate region of the parent plant. The plant is essentially colonial, and if left to grow

in an undisturbed habitat, the colony will increase in size probably mostly as the result of proliferation by the bulb-rhizome. Moreover, most species are very slow-growing. Long distance dispersal is unlikely because the seeds are toxic, and the fruit anything but alluring. Thus, expansion of a species' range must usually progress slowly, and genetic continuity is presumably maintained by the species' pollinators. The pollinators in turn have a limited range and specific ecology. Consideration of these aspects of the biology of the genus leads to the inevitable conclusion that the various species are genetically isolated and that geological barriers can be formidable ones to distribution.

The pattern of speciation in Schoenocaulon can be reduced to two major components: vegetational and geological zones. That is, a species will occupy a particular habitat in soil of particular geologic history. The vegetation of a mountain range rising from about sea level to perhaps 3000 meters may be stratified into several different plant communities. Potentially, a distinct Schoenocaulon species may be found growing in each different zone. In practice, of course, Schoenocaulon species tend to prefer upland habitats to lowland ones. In addition, as the geologic history of the soil varies, the pattern of Schoenocaulon species will vary. Thus, in regions where the geologic history is fairly uniform and the different vegetational zones few, as in the Sierra Madre Occidental of Mexico, there is a correspondingly small number of Schoenocaulon species. Alternatively, when the region is composed of a mosaic of geologic formations, with a myriad of different vegetational zones, such as in

Nueva Galicia or the states of Oaxaca and Puebla, many different species of Schoenocaulon are to be found. In certain cases, the pattern of distribution may not coincide strictly with geological formations, but rather is related to precipitation patterns themselves indirectly determined by topological features. Instances of this occur in the Sierra Madre Oriental of Mexico. The majority of Schoenocaulon species grow in limestone soils, and it is possible that these and other soils harbour special microbes which facilitate the growth of the plants. Species that grow in soils other than limestone, e. g., volcanic or granitic, tend to be morphologically quite distinct and evolutionarily advanced.

Although it is not possible to produce a realistic phylogeny of Schoenocaulon at this time, several evolutionary trends of significance, both within the genus and the Liliaceae are intuitively discernible. These are outlined below:

General Evolutionary Trends Among Temperate Liliaceae

Rhizome	Bulb or corm
Leaves basal	Leaves along inflorescence axis
Inflorescence a raceme with many small flowers	Inflorescence a panicle with few large flowers
Perianth segments all similar & free	Perianth segments in two series & free or all similar & fused
Perianth segments greenish & leathery	Perianth segments brightly colored & petaloid
Nectaries poorly differentiated	Nectaries well differentiated
Apocarpy	Syncarpy
Style & stigmas poorly differentiated & free	Style & stigma well differentiated & progressively more coherent

I will not comment on all of these trends, but will focus on the underground shoot and the flower. For the purposes of the following discussion, the Melanthieae are composed of the following genera: Amianthium, Melanthium, Schoenocaulon, Stenanthium, Veratrum, and Zigadenus; the Narthecieae are composed of: Aletris, Harperocallis, Lophiola, Metanarthecium, Narthecium, Nietneria, Pleea, and Tofieldia. Liliaceae (sensu Dahlgren et al., 1987) including Calochortus are here treated as the Lilioideae.

Although the Melanthieae are not usually considered the most 'archaic' tribe in the Liliaceae (see Krause, 1930) this position being held by the Narthecieae, the Melanthieae are more likely to have given rise to the major evolutionary lines within the lilies. One strong argument for this is that nearly all major features distinguishing advanced lilies may be found within the tribe. No members of the Narthecieae form bulbs, they are strictly rhizomatous. The most archaic tribe in which the bulb makes its appearance is the Melanthieae. Troll (1937) showed how the rhizome of Veratrum could easily become a bulb. Indeed, Meyer (1882) considered Veratrum actually to be bulbous rather than rhizomatous. It is not clear just where the bulb-rhizome of Schoenocaulon fits into this evolutionary scheme. It is quite possible that from a 'rhizome' like that of Veratrum it is a relatively simple evolutionary step to form a bulb. The formation of a bulb from a rhizome may even occur by several different means, thus the bulb-rhizome of Schoenocaulon is not necessarily the 'missing-link'. Certainly at present not enough is

known about the morphogenesis of the underground shoot of Schoenocaulon to infer that this shoot is the archetypal transitional form in the evolutionary progression to all lily bulbs. However; it makes the study of this structure an imperative for the future.

The evolutionary trends within the flowers of temperate lilies were early succinctly stated by Müller (1883). Some of his conclusions are reproduced here:

"The Liliaceae must have once possessed open, regular flowers devoid of honey, visited and cross-fertilized by pollen-seeking insects only. They attained, after dividing into several groups, to the secretion of open, freely accessible, honey, partly secreted by the segments of the perianth, partly by the carpels; and in part they still remain honeyless, and are still crossed only by insects which collect or feed on pollen (*Tulipa*)...Similarly those Liliaceae in which the honey is secreted by the segments of the perianth have in part remained with fully or moderately open flowers, destined for cross-fertilization chiefly by short-lipped insects (Diptera), (*Veratrum*, *Gagea*, *Lloydia*); in others the perianth segments have become approximated without cohesion to form a pendulous bell, fertilized by bees (*Frillaria*); in others the nectaries have become modified into narrow covered grooves, which are accessible to Lepidoptera (*Lilium*); and, finally, in this last genus adaptation has passed from diurnal Lepidoptera to Sphingidae in the case of *Lilium martagon*...

The color of the perianth in Liliaceae must originally have been greenish, as it still is in *Paris*, while the flowers at first made themselves conspicuous to insects by the colour of the reproductive organs. By the selective agency of short-lipped insects, those flowers which had freely-visible honey, and then such as had their honey partially concealed, developed greenish-yellow colours (*Veratrum*), yellow (*Tofieldia*, *Gagea*), greenish-white and white (*Lloydia*, *Anthericum*), and their perianth-segments became devoted to purposes of display. It was only when sand-wasps, bees, long-tongued flies and Lepidoptera began to play a leading part as the fertilising agents, and led to the development of flowers that were no longer accessible to the great host of short-lipped visitors, that red, violet, and blue colours began to be developed through the higher colour-sense of these insects."

H. Müller, The fertilization of flowers. [translated by D'Arcy W. Thompson, 1883]

The flowers of most Schoenocaulon species, by anybody's

reckoning, must be considered relatively primitive within the family. It is clear too, that they primarily offer pollen to insect visitors, and the perianth of many species is inconspicuous. The major advances within the genus are the appearance of petaloid tepals, brightly colored tepals, and well differentiated nectaries. When the former two features are present, the perianth segments are always approximated. The carpels are not well fused within Schoenocaulon; however, in other genera of the tribe, e. g., Zigadenus and Stenanthium, they often are. These two genera sometimes have pendulous flowers as well. In fact, the Melanthieae are probably much more closely related to the Lilioideae than has been previously assumed. Perhaps the major reason this relationship has been overlooked is because most students of Liliaceae evolution have been European, and are unfamiliar with American lilies. Stenanthium frigidum is remarkably similar to several Californian species of Fritillaria. In addition, the chemical data would support a rather closer relationship between the two tribes. As mentioned in the chapter on chemistry, in the Liliaceae steroidal alkaloids are found only in the Melanthieae and in Fritillaria.

It is clear that the Melanthieae and the Lilioideae are separated by a genetic 'jump'; a chasm possibly related to the adaptation of the Lilioideae to more advanced pollinators, as well as to climatic and geological factors.

Schoenocaulon does not appear to have been a seminal genus, giving rise to many other genera. It seems rather to have been an experiment, one which may soon fail at the hands of man and his

four-hooved friends. Nonetheless, it remains an interesting relict
lily from which many lessons concerning the evolution of
monocotyledons may be learned.

Chapter VIII: Ethnobotany

The dried powdered seeds of Schoenocaulon officinale held an important place in the Mexican, Central American, and northern South American Indian and later the European pharmacopoeias. Commonly known as cebadilla or sabadilla, S. officinale is described in the French translation of Monardes's Medicinal plants of America (1619). It is there said to look like barley, probably because of its spikelike raceme, and is illustrated by a figure of Hordeum [Gramineae] (figure 42 B). A better figure is to be found in F. Hernández's Rerum medicarum Novae Hispanae thesaurus (1651) where its Indian name is given as Ytzcuiempatli (figure 42 A).

Early noticed by the European colonists, cebadilla was a considerable object of trade, as were many medicinal plants, among the Indians. The colonists gradually recognized that it possessed properties similar to veratrine, a European drug usually extracted from the rhizome of Veratrum. European recognition of a new drug from Mexico with properties similar to veratrine can be traced at least to the early 18th century where mention of it is made in Lemery's Dictionnaire (1716). As the Europeans were to eventually learn, the source of this drug was the cebadilla seed. A century later, Lindley (1838) mentions that sabadilla seeds were used in making veratrine.

Although S. officinale is commonly considered the medicinal species, other Schoenocaulon species have doubtless served, as it seems that all species have steroidal alkaloids to a greater or lesser degree (see chapter on chemistry). A label note on a specimen of S. comatum collected by Schaffner (536) gives the common name of this

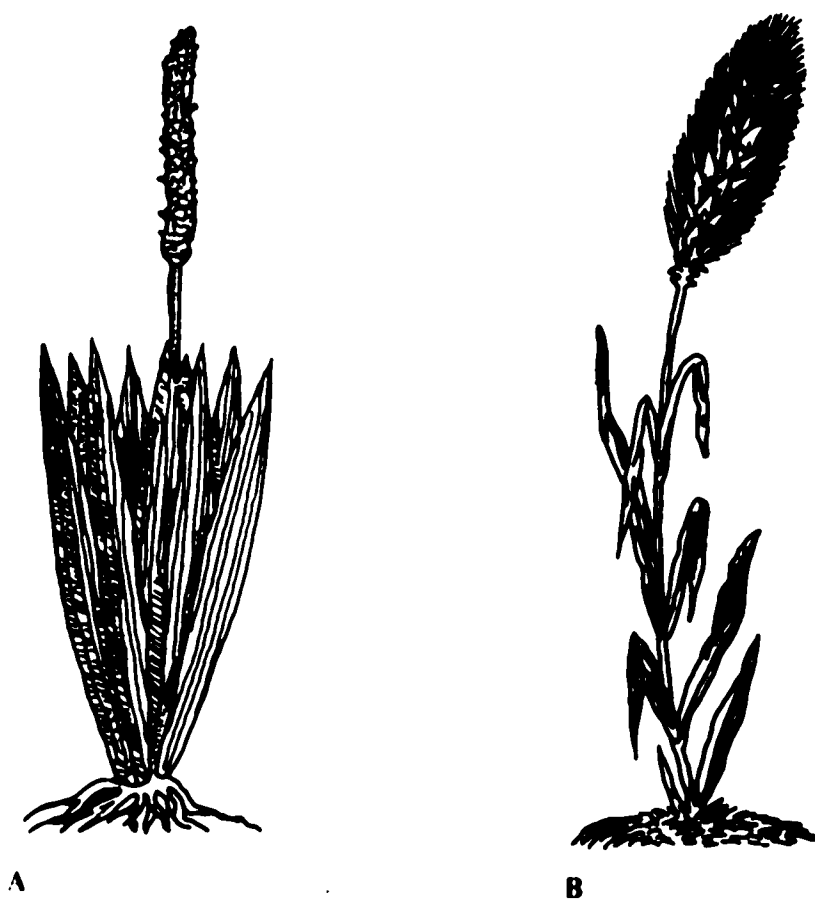


Figure 42. Early illustrations of *Schoenocaulon officinale*.
A, Ytzcuintpatli, after Hernandez (1651); B, Cevadilla,
after Monardes (1619).

species as "matu curros", Spanish for "kills lice", which clearly indicates that species other than S. officinale have been part of the Indian pharmacopoeia. As part of her Huastec Ethnobotany Project, Alcorn made a voucher specimen which proves to be S. ghiesbreghtii (and not S. officinale, as she thought). The label states that it was recognized as a medicinal plant, although not deliberately cultivated. The local name is given as "Cebadilla", which interestingly is the common Spanish name, and not one of Indian derivation.

The dried powdered mature seeds are a rich source of a number of related steroidal alkaloids (see chapter on chemistry), and poisonous. As far as I am aware the seeds were chiefly used for disinfecting deep wounds, and for controlling lice and worms. Europeans used them as an alternative source of 'veratrine', a crude mixture of various steroidal alkaloids, which was used to treat heart and blood pressure complaints. As David Don (Edinburgh New Philos. J. 13: 235. 1832) aptly, if a trifle optimistically, stated: "The Sabadilla or Cevadilla formerly held an important place in the [Indian] Pharmacopoeia, but happily the progressive habits of cleanliness in the people has rendered it now no longer necessary."

These days there are only occasional reports of the use of Schoenocaulon species (see García-Barriga 1974) by indigenous people, as much of the native knowledge concerning the use of this interesting plant has been lost. In the past, however, S. officinale was commonly cultivated for export at mid-elevations in the mountains of Veracruz and near Caracas. Large amounts of seeds were exported to Europe from Venezuela during the first world war to be used against pediculosis,

which was rampant among the soldiers in the trenches; in addition, there are also some label notes suggesting the Germans were attempting to make a poisonous gas from them as well.

To this day, Schoenocaulon officinale remains abundant on the mountains surrounding Caracas. The distribution of this species is curious in that it is by far the widest of all Schoenocaulon species. Another curious fact is that it may be found growing amongst secondary vegetation. These two facts coupled with its being generally the largest species argue strongly for S. officinale having been genetically altered by selection practices of early indigenous cultivators. Most likely it was originally a Mexican species which was improved by those Indians who had developed a use for it and was carried by them or others further south. Although more plastic than most other species of the genus, S. officinale still grows in certain places, such as savannas, better than in others, and is intolerant of grazing by goats. Past cultivation may also have played a rôle in the formation of local races of S. ghiesbreghtii (see discussion under description of that species).

In the early 1940's, some transplantation experiments with S. drummondii (= S. ghiesbreghtii) were conducted by the Texas Agricultural Experiment Station of Texas A & M College at several of their substations. Agronomists there were originally interested in learning whether it might be grown commercially as an ornamental. Scientists at the University of Wisconsin acquired some material of this plant and studied it from the standpoint of its chemistry; they also began to grow it along with S. officinale in greenhouses there.

I do not know what eventually became of the trial propagations by the Texas Agricultural Experiment Substations, but doubtless the advent of World War Two shifted the interests of the University. Nonetheless, a series of classic papers about the chemistry of the tribe Melanthiaceae emerged from the group at Wisconsin, culminating in an article in *Lloydia* entitled "The alkaloids and taxonomy of *Veratrum* and related genera" (see chapter on chemistry).

Today, an extract of the dried powdered seeds of Schoenocaulon officinale in pellet form may be purchased for about \$3.25 and a tincture, which is more concentrated but less used, for a little more, in the homeopathic section of health food stores under the name "sabadilla". The product is manufactured by Boiron Borneman in France, and distributed by the same company in the United States. In books on homeopathy, such as Alain Horvilleur's The Family Guide to Homeopathy (translated by D. Clausen, 1986. Health and Homeopathy Publishing, Inc., Virginia.), sabadilla is usually indicated for the treatment of hayfever. As far as I am aware, this is a novel use for S. officinale seeds. Of course, it is quite possible that Indians did not often have hayfever. Understanding how homeopathic medicine determines the particular use of a substance (usually animal and plant extracts or minerals), is critical to the understanding of how sabadilla has become prescribed for hayfever. In homeopathic medicine, a normal healthy individual is subjected to relatively large doses of a substance and then the drug's effect on the individual is recorded. In the case of sabadilla, the most notable symptoms are violent sneezing, sensitivity (aversion) to the smell of flowers, a

sensation of a lump in the throat concomitant with a constant urge to swallow, and anal itching. The drug is then prescribed in very low dosages for precisely those symptoms it produces in high doses. In the case of sabadilla, this is hayfever. Interestingly, the last symptom relates to intestinal worms (not hayfever!), such as pinworms, the treatment of which by sabadilla is quite traditional. Such a philosophy of drug therapy is not a new one and is recorded for some Indian tribes (Ellen Dean, pers. comm.). The Boiron Borneman company has an agent in France who buys the seeds of Schoenocaulon officinale for them. The agent purchases the seeds in Mexico and Lima, Peru (J. Reversat and P. Carla, pers. comm.). The Peruvian suppliers presumably collect the seed from plants growing in the state of Cuzco. As S. officinale grows in many places in Mexico, research is needed to discover sources of the drug in that country. In any case, it is reassuring to know that there is still a commercial market for this ancient medicinal plant, and that not all knowledge concerning the utility of this plant has receded from the collective human memory.

Other vernacular names

The name "green lily" is recorded for S. drummondii (= S. ghiesbreghtii, "feather-shank" for S. dubium, and "pinyonera" for S. macrocarpum.

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