

This dissertation has been
microfilmed exactly as received 67-1739

FEDDEMA, Charles, 1920-
SYSTEMATIC STUDIES IN THE GENUS SCLEROCARPUS
AND THE GENUS ALDAMA (COMPOSITAE).

The University of Michigan, Ph.D., 1966
Botany

University Microfilms, Inc., Ann Arbor, Michigan

SYSTEMATIC STUDIES IN THE GENUS
SCLEROCARPUS AND THE GENUS
ALDAMA (COMPOSITAE)

by
Charles Peddema

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in the
University of Michigan
1966

Doctoral Committee:

Professor Rogers McVaugh, Chairman
Professor William S. Benninghoff
Associate Professor Peter B. Kaufman
Professor Robert W. Storer
Professor Warren H. Wagner Jr.

SYSTEMATIC STUDIES IN THE GENUS SCLEROCARPUS AND THE
GENUS ALDAMA (COMPOSITAE)

By Charles Feddema

In the subtribe Verbesininae of the Heliantheae (Compositae), there are a number of species in which the receptacular bracts near the margin of the disk completely and closely surround the mature disk achenes and become thickened and ornamented and sometimes hardened at maturity. These species have usually been assigned to Sclerocarpus, Aldama, or Gymnopsis and recent practice has been to assign them all to Sclerocarpus although a treatment of the entire group has never been published.

On the basis of comparative morphological studies of herbarium specimens, observations of living plants in the field and in the greenhouse, hybridizations, and chromosome counts, a systematic treatment of the group is presented. The genus Sclerocarpus and the genus Aldama are found to be distinct and are maintained as separate genera. The species formerly described in Gymnopsis are assignable to Sclerocarpus, Aldama, or other genera.

Formal descriptions of Sclerocarpus and Aldama are made and their relationship to other composite genera is considered. Eight species are recognized in Sclerocarpus, including S. uniserialis which has three varieties, one newly described, and two new combinations are made in the genus. One species is recognized in Aldama with two varieties, including one newly described. Descriptions of the species and varieties in both genera are given as are keys to these taxa. Chromosome counts for the

single species of Aldama and six species of Sclerocarpus are reported, three of these for the first time. The ranges of the species and varieties are described and mapped. All species are illustrated as are some important diagnostic characters of the varieties and the probable evolutionary development of Sclerocarpus is discussed and diagrammed.

PREFACE

The name Sclerocarpus was proposed in 1781 by N. J. Jacquin. The single species of this small genus of the Compositae known to Jacquin was of African origin. Since it was named it has been observed and collected with increasing frequency, chiefly from the Americas where some species are important as local weeds. As more information and more specimens have accumulated, the need for a systematic treatment of these plants has become obvious.

I wish to acknowledge a debt of gratitude to Dr. Rogers McVaugh for inspiration and guidance and to the members of my committee for their assistance in this study. I am indebted to the Horace H. Rackham School of Graduate Studies, University of Michigan, for financial assistance from the Graduate Student Research Fund which made possible field studies in Mexico. I am grateful also to the curators of the following herbaria for lending me specimens and photographs from their significant Texan and Latin American collections. The abbreviations designating these institutions, used here and subsequently in identifying the source of individual specimens, are those of the Index Herbariorum (Lanjouw and Stafleu, 1964).

A Arnold Arboretum, Harvard University, Jamaica Plain,
 Massachusetts

F Chicago Natural History Museum, Chicago, Illinois

GH Gray Herbarium, Harvard University, Cambridge,
 Massachusetts

K Royal Botanic Gardens, Kew, England

MICH University of Michigan, Ann Arbor, Michigan

MO Missouri Botanical Garden, Saint Louis, Missouri

NY New York Botanical Gardens, Bronx, New York

TEX University of Texas, Austin, Texas

US United States National Museum, Washington, D. C.

TABLE OF CONTENTS

	Page
PREFACE.....	11
LIST OF TABLES.....	vi
LIST OF PLATES.....	vii
INTRODUCTION.....	1
KEY TO ALDAMA, SCLEROCARPUS AND RELATED GENERA.....	5
METHODS AND PROCEDURES.....	7
COMPARISON OF SCLEROCARPUS AND ALDAMA.....	11
SCLEROCARPUS.....	16
Chromosome counts.....	16
Hybridization.....	20
Distribution.....	24
Ecology.....	26
DISCUSSION AND CONCLUSIONS.....	29
TAXONOMIC TREATMENT.....	47
Generic description of <u>Sclerocarpus</u>	47
Key to the species of <u>Sclerocarpus</u>	51
Species descriptions.....	56
1. <u>Sclerocarpus multifidus</u>	56
2. <u>Sclerocarpus divaricatus</u>	62
3. <u>Sclerocarpus spatulatus</u>	75
4. <u>Sclerocarpus papposus</u>	81
5. <u>Sclerocarpus sessilifolius</u>	86
6. <u>Sclerocarpus africanus</u>	93
7. <u>Sclerocarpus phyllocephalus</u>	101
8. <u>Sclerocarpus uniserialis</u>	108

TABLE OF CONTENTS - Continued

	Page
Key to the varieties of <u>Sclerocarpus uniserialis</u> ...	110
Descriptions of the varieties of <u>Sclerocarpus uniserialis</u>	112
8a. Variety <u>uniserialis</u>	112
8b. Variety <u>frutescens</u>	119
8c. Variety <u>rubridiscus</u>	126
Excluded species.....	131
Generic description of <u>Aldama</u>	133
Description of <u>Aldama dentata</u>	138
Key to the varieties of <u>Aldama dentata</u>	141
Descriptions of the varieties of <u>Aldama dentata</u>	142
1a. Variety <u>dentata</u>	142
1b. Variety <u>zamorensis</u>	149
Excluded species.....	151
SUMMARY.....	152
BIBLIOGRAPHY.....	155

LIST OF TABLES

Table		Page
I	Comparison of the principal morphological features of <u>Sclerocarpus</u> and <u>Aldama</u>	11
II	Species groups in <u>Sclerocarpus</u> and the principal characters peculiar to them.....	17
III	Chromosome numbers found in species and varieties of <u>Sclerocarpus</u> and <u>Aldama</u>	19

LIST OF PLATES

Plate		Page
I	Photographic reproduction of plate 176 from volume 1 of the <u>Icones Plantarum Rariorum</u> of 1781 by N. J. Jacquin.....	10
II	Morphological and anatomical details of <u>Sclerocarpus</u> and <u>Aldama</u>	13
III	Morphology of trichomes in <u>Sclerocarpus</u>	15
IV	Figure 1. Morphology of trichomes from representative specimens of <u>Aldama dentata</u> ...	40
	Figure 2. Diagram suggesting possible evolutionary relationships in <u>Sclerocarpus</u>	40
V	Distribution maps of <u>S. divaricatus</u> , <u>S. papposus</u> and <u>S. africanus</u>	42
VI	Distribution maps of <u>S. uniserialis</u> , <u>S. spatulatus</u> , <u>S. sessilifolius</u> , and <u>S. multifidus</u>	44
VII	Distribution maps of <u>S. phyllocephalus</u> and <u>Aldama dentata</u>	46
VIII	<u>Sclerocarpus multifidus</u>	55
IX	<u>Sclerocarpus divaricatus</u>	61
X	<u>Sclerocarpus spatulatus</u>	74
XI	<u>Sclerocarpus papposus</u>	80
XII	<u>Sclerocarpus sessilifolius</u>	85
XIII	<u>Sclerocarpus africanus</u>	92
XIV	<u>Sclerocarpus phyllocephalus</u>	100
XV	<u>Sclerocarpus uniserialis</u>	107
XVI	<u>Aldama dentata</u>	137

INTRODUCTION

Species in the subtribe Verbesininae of the Heliantheae (Compositae) form an important element in the floras of Mexico and Central America. In this subtribe there is a group of genera which includes the familiar sunflowers Helianthus and Viguiera and some small genera which are not so well known. All of these have receptacular bracts which tend to fold around the disk achenes. Species in these genera usually have alternate branching, at least in the upper portion of the plant, are predominantly American in distribution, and have perfect, fertile disk flowers. In addition, all have neutral ray flowers with yellow or orange ligules which are usually conspicuous.

Some species in this complex have extremely modified receptacular bracts which completely and tightly enclose the mature disk achenes, and become thickened and ornamented and sometimes strongly hardened. These species usually have been assigned to Sclerocarpus, Aldama or Gymnopsis, and recent practice has been to consider them all as belonging to Sclerocarpus. The problematical status of this group of species with specialized receptacular bracts has been indicated by a number of botanists who have worked on it. A. P. DeCandolle (1836) indicated that Gymnopsis, in which he included species now usually referred to Sclerocarpus, was a "genus male definitum". Torrey and Gray (1842) stated in connection with Gymnopsis that it "seems to include incongruous plants". A century after DeCandolle, Paul C. Standley (1938) wrote of Sclerocarpus

that, "the whole genus seems to be in a chaotic condition. So far as I know, there is available no treatment that brings order out of the apparent chaos exhibited by the usual herbarium material".

Some of the confusion concerning Sclerocarpus is due to the fluid state of generic concepts in the Heliantheae. These concepts have been largely those of major specialists and they have enjoyed a measure of stability only during the lifetime of those who formulated them. Among those who made major contributions in the development of generic concepts in the Compositae were A. P. DeCandolle, Cassini, and Bentham and Hooker. Modern concepts in the genera under consideration are largely those of S. F. Blake who modified and expanded the ideas of B. L. Robinson and J. M. Greenman.

In addition to the problem arising from changing generic concepts, there is one created by the association or confusion of Sclerocarpus and Aldama with genera having no immediate relationship to them. Some genera which have been wrongly associated with Sclerocarpus and Aldama are Melampodium, Madia, Siegesbeckia, Guizotia, Montanoa and Selloa (i.e. Selloa HBK, non Spreng.).

Another problem involving Sclerocarpus and Aldama is presented by the differences between them. Although they have usually been united, they are very different and must be maintained as distinct (see Table I). One of the most important differences between the two genera concerns the unusual fruit type found in Sclerocarpus. This consists of

the achene and the tightly enclosing receptacular bract which becomes thick, hardened and often tubercled. This fruit type is designated a "sclerocarp".

The relationship of Sclerocarpus and Aldama to the other genera in the Heliantheae can be stated only in a general way because of a lack of detailed knowledge of the group. The genus Sclerocarpus appears to be only distantly related to Helianthus, Viguiera and the group of genera associated with them which was outlined by Blake (1918). He considered Viguiera to be "the focus and probable point of origin of a group of seven genera", which included (in addition to Viguiera) Helianthus, Tithonia, Heliomeris, the Gymnolomia of most authors but not of HBK., Hymenostephium, Haplocalymma, and Syncretocarpus. Another genus, Rhysolepis, described later by Blake, must be added to these.

Although these genera are usually assigned to the subtribe Verbesininae, they only superficially resemble Verbesina itself. This genus frequently has winged stems or petioles, fertile or pistillate ray flowers, winged achenes, and occasionally white or cream colored ligules. None of these are characteristic of the genera in the Helianthus-Viguiera group except that Syncretocarpus has somewhat winged achenes. Blake (1918) considered the latter genus to be intermediate between Verbesina and the genera associated with Helianthus and Viguiera.

The genus Aldama is rather closely related to Viguiera. In Aldama, however, the receptacular bracts completely and tightly enclose the disk achenes and become complexly

wrinkled at maturity, whereas in Viguiera the bracts only clasp the achenes loosely and remain smooth or slightly striate. Another genus to which Aldama is related, is Rhysolepis (see Turner, 1962). It differs from the latter genus, however, in the number of veins in the disk corolla, the length of the receptacular bracts in relation to the achene, the degree of enclosure of the receptacular bract about the disk achene, the type of wrinkling of the mature bract, the structure of the involucre bracts and the number of rows of bracts in the involucre, the plane in which the disk achenes are flattened, the type of pappus, the size of the heads, and the general appearance of the plants.

In spite of the differences separating Aldama, Rhysolepis, and Viguiera, all three could be united in a single, more broadly conceived genus, but other genera including Helianthus could also be included in this. For the purposes of this study, practicality dictates the acceptance of these genera as distinct. The possibility of a more inclusive genus in which the present Helianthus and Viguiera might become sections may be explored after future broad reevaluation of generic concepts in the Heliantheae.

The principal characters separating the genera in the Helianthus-Viguiera group as these are currently understood, are emphasized in the following key.

KEY TO SCLEROCARPUS, ALDAMA, AND RELATED GENERA

(Modified from Blake, 1918)

- A. Mature marginal receptacular bracts completely and closely enclosing the disk achene, the margins overlapping adaxially
 - B. Mature marginal receptacular bracts thickened and sclerified, the surface frequently tuberculate
.....Sclerocarpus
 - B. Mature marginal receptacular bracts membranaceous or chartaceous, the surface irregularly wrinkled and pitted.....Aldama
- A. Mature marginal receptacular bracts incompletely or loosely enclosing the disk achene or conduplicate
 - C. Mature marginal receptacular bracts transversely wrinkled.....Rhysolepis
 - C. Mature marginal receptacular bracts smooth or longitudinally striate
 - D. Achenes corky-winged.....Syncretocarpus
 - D. Achenes not corky-winged
 - E. Involucre uniseriate.....Haplocalymma
 - E. Involucre 2-7 — seriate

F. Pappus deciduous, always present, and of two,
usually paleaceous awns and very rarely
including short, intermediate squamellae
.....Helianthus

F. Pappus persistent or none, when present always
including squamellae

G. Peduncles fistulose.....Tithonia

G. Peduncles not fistulose

H. Pappus present

I. Pappus of awns and squamellae, the former
of different shape and texture from the
latter and almost invariably much longer
.....Viguiera

I. Pappus of several subequal membranous
scales.....Hymenostephium

H. Pappus absent

J. Herbaceous perennials, or rarely annuals
(then with the phyllaries strictly
herbaceous); one species with broadly
ovate leaves.....Viguiera

J. Annuals, with the phyllaries 2-seriate,
more or less indurated and ribbed at
base; one species shrubby and with nar-
rowly lanceolate leaves...Hymenostephium

METHODS AND PROCEDURES

A preliminary survey of available herbarium material suggested the desirability of field studies. These were made in July and August, 1961 at which time living plants of most species were observed in their natural environment. The locations of previous collections were visited to determine the present condition of populations known to have existed in the past, specimens were collected to augment meager study material and provide a better understanding of the variation within the species, cytological material was preserved and seeds were collected. Areas near the known limits of the ranges of the species were examined in order to verify or redefine these boundaries. Areas within these ranges from which no collections were known were examined to determine the nature of the occurrence and coverage of the species within their ranges. In the herbarium, more than 800 specimens were examined and morphological studies made. Measurements of bracts, flowers and flower parts were made from material soaked in water, except that fresh material was measured when available. Seeds collected in Texas and Mexico and others received from Africa and West Pakistan were germinated in flats and subsequently transplanted to pots and grown under approximately uniform culture conditions at the University of Michigan Botanical Gardens. A number of hybridizations were attempted and some success was achieved. A chromatographic analysis of leaf extracts was made by Dr. Rainer Scora, but results were inconclusive. Chromosome counts

were made for all but two species from microspore mother-cell squashes. Buds for all chromosome counts were collected in the field except for those of Sclerocarpus africanus. The count for this species was made from microsporocyte material obtained from plants grown from seeds of a specimen (H. Wild 5760) collected in Rhodesia and furnished by the collector. Buds for the chromosome counts were killed and fixed in Newcomer's solution. Young anthers were removed and squashed in acetocarmine and mounted in Hoyer's medium.

PLATE I

Photographic reproduction of plate 176 from volume 1 of the
Icones Plantarum Rariorum of 1781 by N. J. Jacquin.



Sclerocarpus africanus.

Act. helv. vol. 9.

Table I. Comparison of principal morphological features of Sclerocarpus and Aldama*

	Aldama	Sclerocarpus
Leaves	Blade lanceolate Margin entire or minutely denticulate Petioles short	Blade ovate-trullate or deltoid Margin coarsely toothed Petioles long
Involucre	Biseriate Bracts appressed to flowers, brownish or dark green	Uniseriate or biseriate Bracts spreading or reflexed, green like the leaves
Receptacle	Shallowly convex	Conical or ovoid
Ray Flowers	Ligules narrow, linear or oblong Tube short Achenes thin, flat, chambered	Ligules ovate-circular Tube long Achenes usually fleshy throughout
Disk Flowers		
Corolla	Ten-nerved Lobes short, deltoid, unbearded	Five-nerved Lobes long, lanceolate, bearded
Anthers	Brown Exserted from corolla at anthesis Connective short, deltoid	Yellow Retained in corolla at anthesis Connective long, lanceolate
Style	Short Branches flattened, broadest below apex	Long Branches terete, attenuate
Achenes	Marginal ones often obcompressed, trigonous	Marginal ones usually laterally compressed
Mature marginal receptacular bracts	Thin Chartaceous or pithy Surface irregularly wrinkled or pitted	Thick Hard or fibrous Surface often with raised tubercles

* Quantitative characters are described in relative terms. Exact dimensions of the organs are indicated in the formal taxonomic descriptions.

PLATE II

MORPHOLOGICAL AND ANATOMICAL DETAILS OF SCLEROCARPUS AND
ALDAMA

- Fig. 1. Gross leaf venation, x 0.5. S. uniserialis.
 Fig. 2. Upper leaf epidermis, x 100. S. papposus.
 Fig. 3. Upper leaf epidermis, x 100. A. dentata.
 Fig. 4. Style, x 5. S. uniserialis.
 Fig. 5. Style, x 5. A. dentata.
 Fig. 6. Apex of styler branch, lateral view, x 50.
S. divaricatus.
 Fig. 7. Styler branch, lateral view, x 50. A. dentata.
 Fig. 8. Styler branch, outside view, x 50. A. dentata.
 Fig. 9. Styler branch, lateral view, x 50. S. africanus.
 Fig. 10. Longisection through sclerocarp, x 10.
S. spatulatus.
 Fig. 11. Corolla venation, x 10. A. dentata.
 Fig. 12. Corolla venation, x 10. S. sessilifolius.
 Fig. 13. Transection through sclerocarp, x 10.
S. multifidus.
 Fig. 14. Transection through sclerocarp, x 10.
S. uniserialis.
 Fig. 15. Anthers, x 12. A. dentata.
 Fig. 16. Anthers, x 12. S. divaricatus.
 Fig. 17. Transection through sclerocarp, x 100. A. dentata.
 Fig. 18. Transection through sclerocarp, x 100.
S. uniserialis.
 Fig. 19. Lobe of disk corolla, inner surface, x 25.
S. sessilifolius.

Specimens illustrated: A. dentata, Feddema 1556 (MICH).
S. africanus (living plant, offspring of H. Wild 5760).
S. divaricatus, Feddema 1555 (MICH). S. multifidus, Feddema
 1664 (MICH). S. papposus, Mexia 8707 (MICH). S.
sessilifolius, McVaugh 19082 (MICH). S. spatulatus, Feddema
 1777 (MICH). S. uniserialis, Feddema 1468 (MICH).

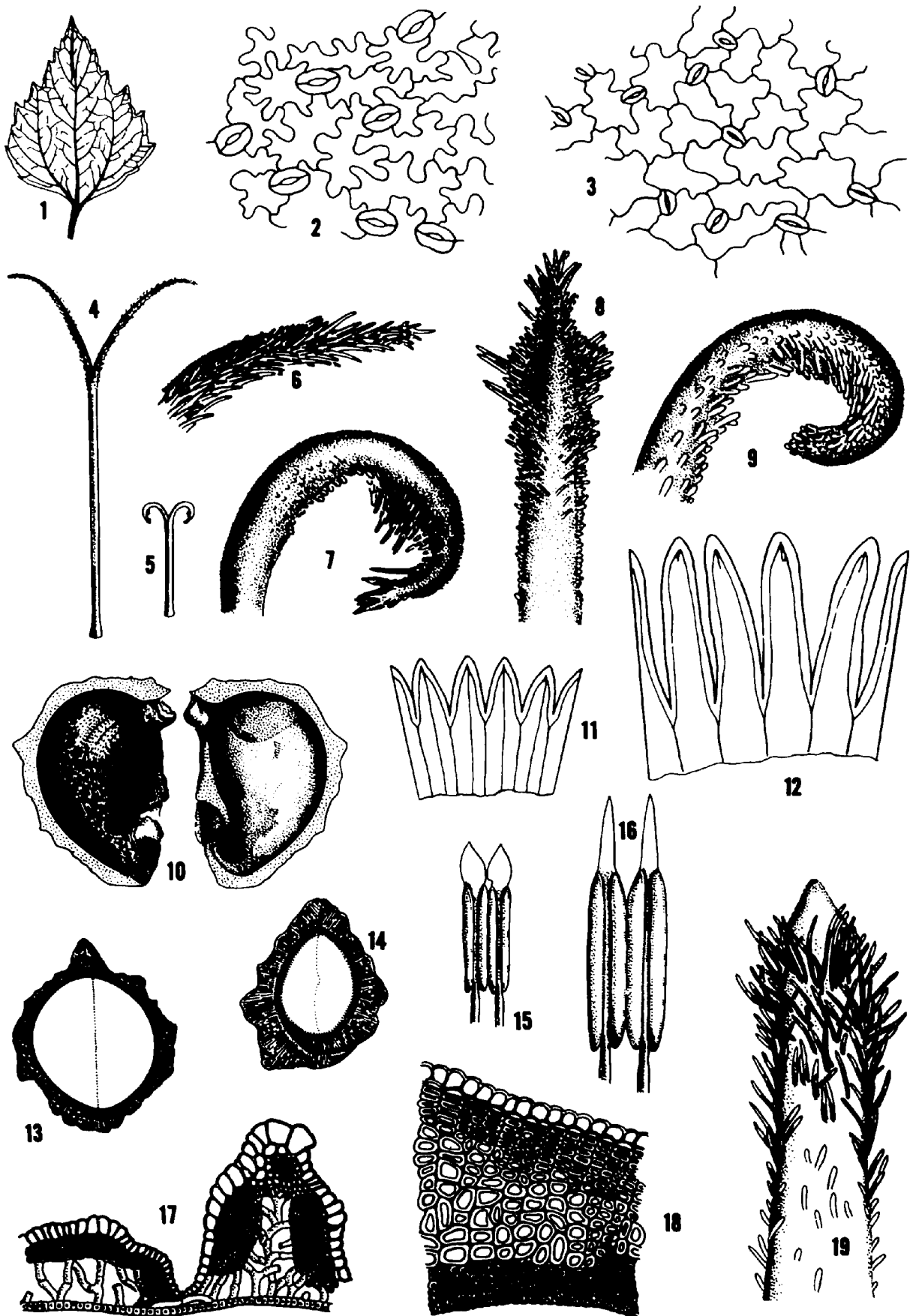


PLATE III

MORPHOLOGY OF TRICHOMES FOUND IN SCLEROCARPUS

Fig. 1. Trichomes from main stem and branches, x 50.

Fig. 2. Trichomes from adaxial surface of leaf, x 50.

Fig. 3. Trichomes from inner surface of corolla, near middle of the lobe (beard), x 100. 3g illustrates trichomes from various portions of the beard. Trichomes from the distal portion of the beard are illustrated at the upper part of the figure, while trichomes from the proximal portion of the beard are illustrated at the bottom of the figure.

Fig. 4. Trichomes from abaxial surface of leaf, x 50.

Fig. 5. Trichomes from apex of corolla lobe, outer surface, x 100.

Fig. 6. Trichomes from various portions of the disk corolla, x 100, as follows:

6a, outer surface of tube, near base of the lobe;

6a', inner surface of tube, below base of the lobe;

6b, outer surface of lobe, below apex;

6d, outer surface of tube, below base of lobe;

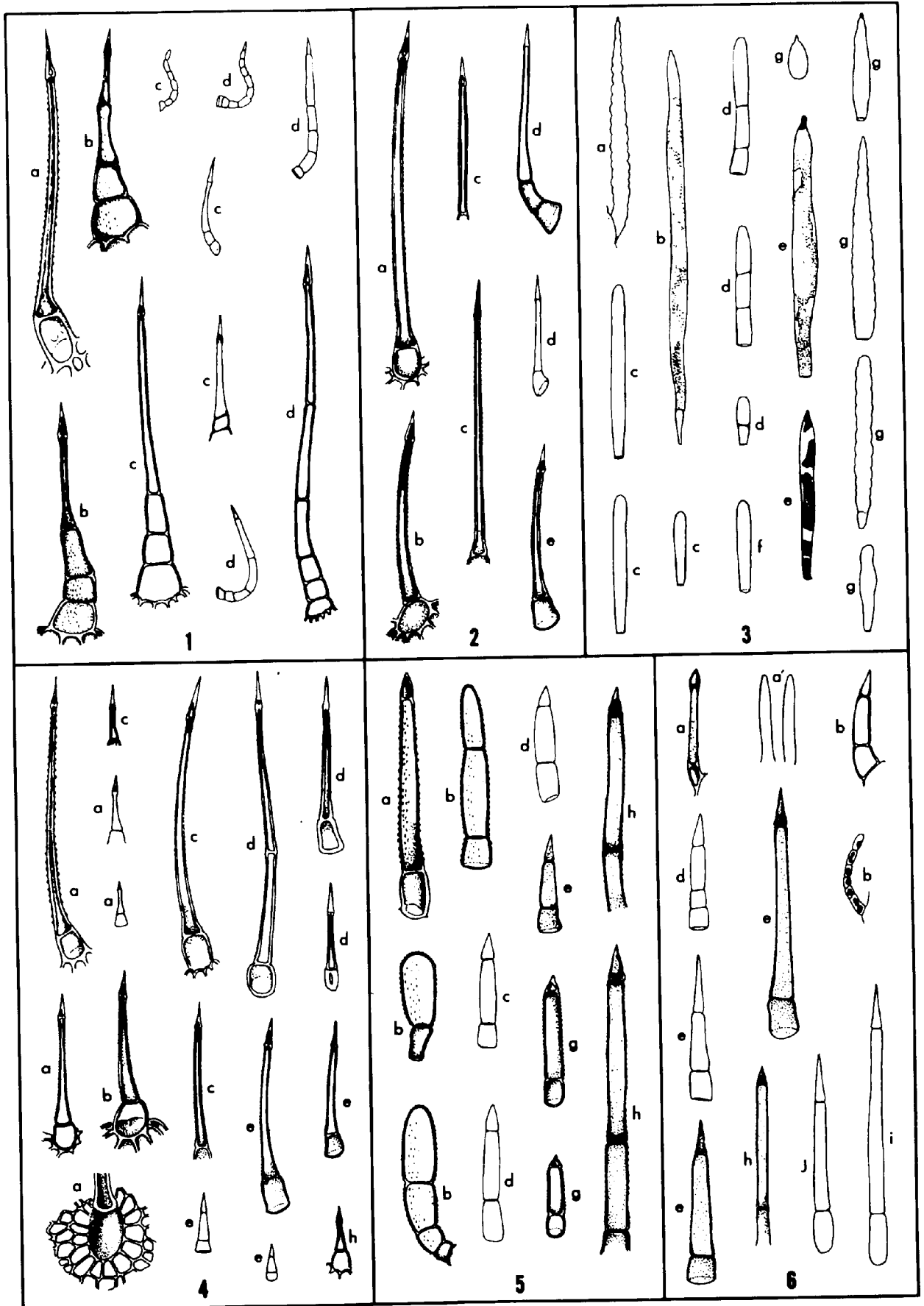
6e, outer surface of lobe, below apex;

6h, outer surface of lobe, at base;

6i, 6j, outer surface of lobe, near middle.

Specimens from which trichomes are illustrated:

a, Sclerocarpus uniserialis var. uniserialis, Feddema 1468 (MICH); b, Sclerocarpus sessilifolius, Feddema 1758 (MICH); c, Sclerocarpus phyllocephalus, P. C. Standley 21326 (F); d, Sclerocarpus africanus (Drawn from plant grown from seeds of H. Wild 5760); e, Sclerocarpus divaricatus, Feddema 1555 (MICH); f, Sclerocarpus africanus, H. H. Smith 510 (MICH); g, Sclerocarpus papposus, I. Mexia 8707 (GH); h, Sclerocarpus uniserialis var. rubridiscus, Feddema 1650 (MICH); i, Sclerocarpus multifidus, Feddema 1621 (MICH); j, Sclerocarpus spatulatus, Feddema 1777 (MICH).



SCLEROCARPUS

The species of Sclerocarpus can be arranged naturally in four groups on the basis of their morphology. The recognition of these groups aids in interpreting the evolution of the genus although they are not accorded formal taxonomic status. A unique species, Sclerocarpus sessilifolius, differs from all others in being a procumbent woody perennial with sessile or nearly sessile, entire or minutely denticulate, lanceolate leaves. Two very similar species, Sclerocarpus africanus and S. phyllocephalus, are peculiar in having leaf-like outer phyllaries, few and very small ray flowers with hollow, sterile achenes, and sclerocarps with transverse grooves and ridges. A third group of species consists of Sclerocarpus papposus and S. uniserialis, the latter considered to include three varieties. These two species usually have disk corollas with reddish or purple areas and a beard with torose trichomes. Both Sclerocarpus papposus and S. uniserialis var. uniserialis have long and straight beaked sclerocarps with low, uniform simple tubercles. The fourth group consists of Sclerocarpus multifidus, S. spatulatus, and S. divaricatus. These species all have unbeaked sclerocarps, ovoid-conical receptacles and beards in the disk corollas composed of black hairs with an apical knob. (see Table II.)

CHROMOSOME COUNTS

Chromosome counts from available material strongly support the morphological evidence for four groups of species in the genus. The groups described above, as far

Table II. Species groups in Sclerocarpus and the principal characters peculiar to them

Species	Chromosome number (n)	Characters peculiar to group
<u>S. sessilifolius</u>	14	Woody perennial Habit procumbent Blades entire or minutely denticulate Sclerocarps longitudinally ribbed
<u>S. africanus</u>	18	Outer phyllaries similar to leaves
<u>S. phyllocephalus</u>	?	Ray flowers small Ray achenes with locule Sclerocarps transversely ridged dorsally
<u>S. uniserialis</u>		Disk corollas with reddish areas and torose
var. <u>uniserialis</u>	12	trichomes in beard
var. <u>frutescens</u>	12	Receptacles long-conical
var. <u>rubridiscus</u>	12	Sclerocarps long-beaked
<u>S. papposus</u>	?	
<u>S. multifidus</u>	11	Disk corolla black bearded
<u>S. spatulatus</u>	11	Achenes subterete, recurved
<u>S. divaricatus</u>	11	Marginal sclerocarps beakless, the tubercles conical Receptacle ovoid

as the species now known, have haploid numbers of 14, 18, 12, 11, respectively (see Tables II, III). No previous counts have been reported for Sclerocarpus africanus ($n = 18$). The close morphological similarity of this species to Sclerocarpus phyllocephalus suggests a probable number of 18 for the latter. Turner, Powell and King (1962) reported counts of $n = 11$ for specimens which they tentatively identified as Sclerocarpus phyllocephalus. These reports were based on specimens of Sclerocarpus divaricatus (see below). The count for Sclerocarpus sessilifolius was $n = 14$, confirming a report by Turner, Powell and King (1962). These authors reported counts of $n = 12$ for King 3533, identified as S. dentatus and King 2936, identified as S. cf. frutescens. They also reported a count of $n = 11$ for King 3485, identified as S. dentatus. These specimens are actually introgressants between S. uniserialis var. frutescens and var. rubridiscus. The same authors also reported counts of $n = 12$ for King 4086, 4118, 4094, and 4233 and for Powell & Edmondson 506, all identified as Sclerocarpus dentatus. These are actually specimens of S. uniserialis var. frutescens. Turner (1960), reported a count of $n = 12$ for Turner et al. 3133, determined as Sclerocarpus uniserialis. This is a specimen of S. uniserialis var. uniserialis.

The closely related species, S. multifidus, S. spatulatus, and S. divaricatus were found to have a haploid number of $n = 11$. No previous counts are known for S. multifidus and S. spatulatus, but counts of $n = 11$ were

Table III. Chromosome numbers found in species and varieties of Sclerocarpus and Aldama (from pollen mother cell squashes)

Taxon	Haploid number	Specimen
<u>S. multifidus</u>	11	MORELOS: near Amacuzac, <u>Feddema 1621</u>
<u>S. divaricatus</u>	11	VERACRUZ: 30 km SE of Córdoba, <u>Feddema 1555</u>
<u>S. spatulatus</u>	11	SONORA: 6 km W of Alamos, <u>Feddema 1777</u>
<u>S. sessilifolius</u>	14	NAYARIT: near Santa María del Oro, <u>Feddema 1758</u>
<u>S. africanus</u>	18	Counted from plant grown from seed of H. Wild 5760, collected in Rhodesia
<u>S. uniserialis</u> var. <u>uniserialis</u>	12	TEXAS: Brooks Co.; 5 mi N of Encino, <u>Feddema 1468</u>
<u>S. uniserialis</u> var. <u>frutescens</u>	12	SAN LUIS POTOSI: 36 mi SW of Tamazunchale, <u>Feddema 1502</u>
<u>S. uniserialis</u> aff. var. <u>rubridiscus</u>	12	MICHOACAN: 8 km SW of Nueva Italia, <u>Feddema 1710</u>
<u>S. uniserialis</u> var. <u>frutescens</u> X var. <u>rubridiscus</u>	12	OAXACA: 24 km NW of Tehuantepec, <u>Feddema 1596</u>
<u>Aldama dentata</u> var. <u>dentata</u>	17	VERACRUZ: 9 km SW of Nogales, <u>Feddema 1541</u>
<u>Aldama dentata</u> var. <u>zamorensis</u>	17	MICHOACAN: 27 km SE of Zamora, <u>Feddema 1724</u>

reported by Turner, Powell and King (1962) for King 2733, identified as S. cf. divaricatus and for King 3126 and 3372, identified as S. cf. phyllocephalus. Another count of $n = 11$ was made by the above workers as indicated on the label of King 5339 (MICH). They also reported a count of $n = 12$, however, for King 3440, identified as S. cf. phyllocephalus. All of these are specimens of S. divaricatus. The chromosome counts made and the specimens of the plants from which they were made are indicated in Table III. Voucher specimens are on file at The University of Michigan Herbarium.

HYBRIDIZATION

The ability of members of two populations to hybridize, the extent to which this takes place or can be made to take place, and the degree of fertility of any resulting hybrids may furnish evidence of the degree of relationship between the two populations and thus aid in arriving at a more natural systematic arrangement. The possibility for hybridization is to be expected between members of populations which are morphologically similar and have the same chromosome numbers. Two such morphologically similar species, Sclerocarpus africanus and S. phyllocephalus, are nowhere sympatric and neither confirmed nor suspected hybrids are known. A species with a unique morphology and chromosome number, Sclerocarpus sessilifolius, has a range that is included within that of S. divaricatus and although the distribution of both is discontinuous within their principal ranges, plants of these species could be expected

to exist within effective pollinating range. No hybrids between them are known nor are they to be expected. Of the three closely related species with the same chromosome number ($n = 11$), Sclerocarpus multifidus, S. divaricatus and S. spatulatus, the last named species is outside the range of the others. Sclerocarpus multifidus and S. divaricatus have ranges which are contiguous or overlapping in western Guerrero and eastern Michoacan. A collection of S. divaricatus, Leavenworth & Hoogstraal 1575 (NY), from Apatzingán, is a sheet with five small plants, some of which have grayish leaves with long teeth or lobes and narrow phyllaries, suggesting introgressive hybridization with S. multifidus. Attempts to cross these two species in the laboratory were inconclusive, but seeds from one specimen of S. multifidus which had grown in the greenhouse in close proximity to plants of S. divaricatus and open to random pollination by bees, wind and gravity, produced plants with phyllaries clearly broader than those normally found in S. multifidus. A few leaves on this plant were not dissected but had long, lobe-like teeth and the large cauline leaves had somewhat broader lobes than the average found in S. multifidus. It is possible that this plant, Feddema 3000 (MICH), is a hybrid between these two species.

Of the two closely related species, Sclerocarpus papposus and S. uniserialis, the former is rare and known from only three collections. One of these collections of S. papposus is from Taxco, Guerrero, where it is presumably sympatric with S. uniserialis var. rubridiscus. These

species were not observed growing together, nor are hybrids between them known to exist. Of the three closely related varieties of Sclerocarpus uniserialis, var. uniserialis is geographically isolated from var. frutescens, its nearest relative morphologically and spatially, by at least 150 miles, and no natural hybrids between these two varieties or between var. uniserialis and var. rubridiscus are known. Var. frutescens and var. rubridiscus, on the other hand, have ranges which overlap or are contiguous in areas of Puebla, Morelos, Oaxaca and probably in the poorly known eastern regions of Guerrero. A number of collections of the species from these areas clearly show characters of both varieties and are considered to be the result of recent hybridization and introgression between them. In the greenhouse, a number of successful crosses were made between the different varieties of Sclerocarpus uniserialis. Plants of the three varieties were crossed with each other. Seeds developed on these plants were planted in flats and later transplanted to pots, and on reaching maturity, were examined for characters not found in the plants on which the seeds developed, but which were found on the pollen contributing parents.

Seeds from a plant which was the offspring of a specimen of var. Frutescens (Feddema 1501), which has yellow disk flowers and strongly bent sclerocarps, developed into plants with the reddish brown disk flowers and straight sclerocarps of the plant with which it was crossed, an offspring of var. uniserialis (Feddema 1468). Similarly,

plants of the red form of var. uniserialis (offspring of Feddema 1468), were crossed with those of var. rubridiscus (offspring of Feddema 1650). Progeny from seeds on the latter, exhibited the brownish red disk flowers, nearly straight sclerocarps with very small tubercles and long involucral bracts of the former, the pollen contributing plant. In addition, the offspring were tall plants over one meter high like var. uniserialis rather than approximately one-third that height similar to the parent on which the seeds were formed. The reciprocal cross of these two varieties produced plants having the strongly bent sclerocarps with large tubercles and purple receptacular bracts of var. rubridiscus, the male parent.

A plant grown from seeds of Feddema 1607, a natural hybrid or introgressant between var. frutescens and var. rubridiscus, was crossed with a plant of var. frutescens (grown from seeds of Feddema 1489). Seeds from the heads on var. frutescens developed into plants with the coarsely tubercled sclerocarps of var. rubridiscus which were also observed on the pollen contributing parent. The results of these crosses indicate complete compatibility between the different varieties of S. uniserialis and a close relationship and probably a recent derivation from a common ancestor.

Specimens of Sclerocarpus uniserialis from western Guerrero and eastern Michoacan display an assortment of characters of var. uniserialis and var. rubridiscus. These

can probably be best explained as relicts of a parental population from which the modern varieties developed.

A summary of these crosses and the designations of the resulting hybrids, of which voucher specimens are filed at the University of Michigan Herbarium, are as follows:

Sclerocarpus uniserialis var. rubridiscus (grown from seed of Feddema 1650) X S. uniserialis var. uniserialis (grown from seed of Feddema 1468). This hybrid is designated Feddema 2936.

Sclerocarpus uniserialis var. uniserialis (grown from seeds of Feddema 1468) X S. uniserialis var. rubridiscus (grown from seeds of Feddema 1650), Feddema 2953.

Sclerocarpus uniserialis var. rubridiscus (grown from seeds of Feddema 1650) X S. uniserialis var. uniserialis (grown from seeds of Feddema 1468), Feddema 2936.

Sclerocarpus uniserialis var. rubridiscus X var. frutescens (grown from seeds of Feddema 1607, a natural hybrid) X S. uniserialis var. frutescens (grown from seeds of Feddema 1489), Feddema 2937.

DISTRIBUTION

With one notable exception, Sclerocarpus is limited in its distribution to the North American subtropical region between ten and thirty degrees north latitude. The exception, Sclerocarpus africanus, is a disjunct species with a major distribution across tropical Africa, a well developed but isolated population in West Pakistan and northern India. Small isolated populations of this species on St. Thomas (American Virgin Islands), and in coastal Venezuela and

Colombia suggest introductions by seaborne commerce. Of the two species of Sclerocarpus presumably adventive around the mouth of the Magdalena River in Colombia, S. africanus has apparently become well established since it was first collected approximately sixty-five years ago.

There are several rather narrowly endemic species of Sclerocarpus, especially in western Mexico, and of the two widely ranging species, one, S. uniserialis, consists of three varieties whose ranges are somewhat restricted. Variety frutescens, whose main range is in northeast Mexico, has isolated populations in Yucatan, Campeche, and Chiapas. The wide-ranging Sclerocarpus divaricatus consists of eastern and western populations which are essentially isolated from each other and have developed minor morphological differences. Isolated populations of this species also occur in Yucatán, Chiapas, Campeche and northern South America.

The distribution of Sclerocarpus indicates that it is of American origin as all but one species occur naturally in tropical America. The one exception, S. africanus, is most closely related to S. phyllocephalus and conceivably might have been derived from it by long distance dispersal and subsequent speciation. This would have been facilitated by the inbreeding tendencies in the genus which permit one successful propagule to be ancestral to a whole species. Such a dispersal presumably occurred long ago judging by the differentiation which has resulted and by the wide range of the plant in the Old World. Secondary introduction of

the species to the New World can be considered a recent event on the basis of its very restricted distribution here and the similarity of plants here to those in the Old World.

ECOLOGY

Plants of the genus Sclerocarpus occur at elevations from sea level to 2000 meters but are most frequently found near the coasts or at elevations below 500 meters. They are adapted to open areas and well deserve the name "mirasol" by which they are usually known. Most members of the genus are intimately associated with areas disturbed by man's activity and his agriculture and are most frequently encountered along highways, railroads and fences or as weeds in grainfields.

The life cycle of Sclerocarpus uniserialis var. rubridiscus is typical of a species closely related to the agricultural pattern in the region where it is most abundant. Seeds of this variety remain dormant after dispersal in the grainfields until the following rainy season when maize is planted. Plants of Sclerocarpus do not reach maturity until after active cultivation of the maize ceases. When the stalks of maize are cut, the weeds mature and dominate the fallow fields until the next growing season. In August, the valley of Chilpancingo, Guerrero, including the fields and adjacent roadsides, was observed to be an almost unbroken sweep of color due to aspect dominance of this variety in flower. An examination of a typical field in this area indicated that bare ground occupied an estimated 50% of the area. Sclerocarpus

uniserialis var. rubridiscus provided almost 30% of cover, one species of Melampodium and Heliotropium provided a total of 10% of cover and the remainder was provided by several species of weedy genera such as Euphorbia, Sanvitalia and Paspalum, each of which accounted for less than 5%.

In many areas Sclerocarpus is subjected to grazing pressures. Mrs. Ynez Mexia indicated on specimen labels that S. papposus is grazed by goats when the plants are young, especially when grass is scarce. In the region around the city of Tehuantepec, Oaxaca, Sclerocarpus uniserialis var. frutescens is often found with the terminal portion of the plant missing and only lower branches remaining. In Hidalgo, near Jacala, the same variety was found with the entire plant grazed except for one or a very few basal branches. Apparently adapted to grazing, S. uniserialis var. frutescens sends up shoots from the base of the stem and from lower branches, presumably from lateral buds, and also develops new adventitious roots in the same parts of the plant. In heavily grazed areas near Tepic, Nayarit, Sclerocarpus sessilifolius was observed surviving successfully beneath or close beside clumps of Baccharis while its branches grew in and between those of the shrub. The fact that the shrub was scarcely grazed suggests that it was unpalatable to livestock.

Several species of Sclerocarpus were observed in the field and in the greenhouse being visited by bees. Some in the field were also visited by beetles. Insect visits provide the probable means of cross-pollination for the species.

Several species are attacked by insects which lay their eggs in the young ovary of the disk flower. The egg hatches and the young larva feeds on the maturing ovule and later emerges through a hole which it makes in the wall of the sclerocarp.

When plants of the genus are mature, the sclerocarps are shed from the disk and fall to the ground. They are not widely dispersed at this time but rains of the strength frequently found where the genus occurs could be expected to bring about some dispersal. It is expected that animals must also play a role in this process. After the sclerocarps are shed, they usually remain dormant for some time. The need for dormancy or an after-ripening period was indicated in the species tested. Seeds of S. multifidus, S. divaricatus and S. uniserialis var. uniserialis were sown approximately two months after harvesting with no resulting germination. Seeds from the same lots were sown under approximately similar conditions seven months after harvesting with a high percentage of germination resulting. A mechanism preventing germination after occasional rains in a normally dry season would aid in the survival of a species.

DISCUSSION AND CONCLUSIONS

Although the Heliantheae are considered by most modern specialists to be the most primitive tribe in the Compositae (see Cronquist, 1955), Sclerocarpus must be considered a relatively specialized derivative from a helianthoid ancestor which had yellow, perfect disk flowers and neutral, ligulate ray flowers and which may have resembled modern Helianthus or Viguiera. The enfolding of disk flowers and achenes by the receptacular bracts is a phenomenon which is found widely in other genera and tribes of the Compositae. It is, in fact, to be expected if the bract is broad and many flowers are crowded on the receptacle. The complete and tight enclosure of the mature marginal disk achenes, as it occurs in Sclerocarpus and Aldama, may be due to parallel development in the two genera or may indicate derivation from a common ancestor. The further development, however, in the anatomical structure and the form and surface ornamentation of the bract in the two genera is highly divergent.

The great similarity in the development of the sclerocarp in all species of Sclerocarpus suggests that they are derived from a common ancestor in which the receptacular bract completely enclosed the disk achene and had already become somewhat thickened and sclerified. Speciation, occurring along a few main lines in the modification of the receptacular bracts and other vegetative and reproductive organs, produced the modern genus.

The adaptive significance of the highly modified receptacular bract in Sclerocarpus can be only a matter for speculation. Small (1918), and Cronquist (1955), suggest that orthogenesis operates in the Compositae in bringing about extreme development of certain structures beyond the requirements of adaptation for survival. The nut-like sclerocarp in Sclerocarpus, however, can be assumed to have a protective value, as it is usually tough, thick and frequently "stony". It provides a covering for the seed in addition to the integuments of the ovule and the ovary wall, all of which are thin. The thickened bract and plug of oily tissue sealing the base of the bract may be factors in reducing evaporation from the tissues of the seed, although the apex of the bract is somewhat exposed. Of interest here, as an indication of an evolutionary trend toward a more protective function for the bract, is the presence in some specimens of Sclerocarpus multifidus, of bracts in which the margins do not overlap, but are completely fused in embryonic development to form a continuous tube around the base of the achene.

The vegetative receptacular bract assumes some of the characters of a fruit in that its complete development on the margin of the disk is dependent upon and closely associated with the pollination of the flowers and the fertilization and development of the enclosed ovule. Bracts surrounding flowers in which these events have not occurred are conspicuously undeveloped in heads of normally

developing bracts. Thin, blade-like bracts at the center of the receptacle often enclose abortive or undeveloped achenes.

Of possible evolutionary significance in Sclerocarpus is the presence of two morphological and presumably physiological gradients associated with the inflorescence. One of these gradients is observed in the degree of development of the receptacular bracts from the center to the margin of the disk. Those at the center of the disk remain thin, tubular and blade-like and loosely enclose the achene, while those at the margin of the disk become thickened, complex in form and surface sculpturing, and tightly enclose the achene. Bracts from the center of the disk to the margin often show a gradual change in form suggesting both a heteroblastic and phylogenetic series. Another morphological series is observable in the gradual reduction in size and form of the leafy appendages, from the leaves of the stem, through the leafy bracts sometimes found on the peduncle, to the involucre bracts. In Sclerocarpus africanus and S. phyllocephalus, the indicated gradient is very sharp. The outer involucre bracts are often entirely leafy, while within the involucre itself there is a graduated series showing the reduction of the blade to insignificance at the apex of the innermost bracts.

In species with more than one complete whorl of involucre bracts, the outer are slightly more leaflike than the inner. An interesting abnormality is observed in a specimen of Sclerocarpus divaricatus from El Salvador, P. C. Standley

23195 (US), in which the involucre is composed of several whorls of crowded bracts instead of the usual number of five to seven bracts occurring in a single whorl. Whether or not this may be accepted as an atavism indicating derivation of the species from an ancestor with a multi-seriate involucre, it does suggest a potential for flexibility in the number, form and arrangement of the leaf-derived structures associated with the inflorescence.

In Sclerocarpus there are only a small number of closely related species with few positive evolutionary trends indicated within the group. Among the evolutionary specializations observed in Sclerocarpus, however, is the development of pinnatifid leaves in Sclerocarpus multifidus only. This is certainly a condition derived from the toothed condition found in all other species. Another evolutionary tendency in the genus is suggested by the presence of hollow ray achenes in two species while all others are solid. The chamber in the ray achenes of Sclerocarpus africanus and S. phyllocephalus suggests the locule in perfect disk flowers from which ray flowers in the Compositae are generally held to be derived. The disappearance of the locule in most species may be a further modification of the ray flower from the perfect condition. Occasionally a ray flower is observed bearing a style, an atavism suggesting a sexual ancestral condition.

The 5-nerved condition generally observed in the disk corollas of Sclerocarpus is believed to be derived from the 10-nerved condition (see Carlquist, 1961). Occasionally,

in Sclerocarpus africanus, there may be one or more lobes with a midvein. In S. sessilifolius, the apex of the lobe often shows the beginning of a midvein which soon anastomoses with the lateral vein. The variations in the trichomes of the beard on the lobes of the disk corolla show other specializations within the genus and are characteristic of the four species groups. The simplest trichomes are found in Sclerocarpus africanus and S. phyllocephalus, two species which show other primitive characters. In these species, the trichomes of the beard are colorless or faintly yellow, short, cylindrical with straight walls and a uniformly rounded apex. In Sclerocarpus divaricatus, S. spatulatus, S. multifidus and S. sessilifolius, the trichomes in the beard have an apical knob and are black due to substances in the cells which are not found in surrounding epidermal cells. The latter condition is considered to be an evolutionary specialization by Netolitsky (see Carlquist, 1961). In Sclerocarpus sessilifolius, the beard trichomes are long and sinuate, in S. uniserialis they are torose, and in var. rubridiscus they are reddish apparently due to anthocyanins dissolved in the cell sap. In S. papposus, the form of the trichomes in the beard shows a gradual modification from the upper margin of the beard to the lower. Trichomes at the upper margin of the beard are short, ovoid, and have an apical protuberance. Trichomes near the middle of the beard closely resemble those of S. uniserialis in form, while those at the base of the beard are shorter, narrow at base

and with only few swellings and constrictions. This series suggests that the long complex trichomes in the beard of most species are derived from the short, knobbed papillae which are found at the apex of the disk corollae in all species. (See Plates III and IV for illustrations of trichome types.)

The receptacular bracts found at the margin of the disk, which are probably leaf-derived, have become differentially specialized within the genus. The loss of the apex of the bract has resulted in an unbeaked sclerocarp in Sclerocarpus divaricatus, S. spatulatus, and S. multifidus. In some species the beak of the sclerocarp, i.e. the apex of the receptacular bract, is bent adaxially. This is a specialization from a primitive cylindrical or conical sclerocarp which would result from the infolding of a blade-like bract around a straight achene of the type commonly found in the Compositae. The marginal sclerocarp in Sclerocarpus uniserialis var. uniserialis is nearly straight and tubular and may more closely resemble the primitive form than those of other species, but the preponderance of species with bent sclerocarps suggests that the straight sclerocarps may be secondarily derived. Another specialization in the sclerocarp is observed in the variety of surface ornamentation found in the genus. Ribs and tubercles of different size and form are characteristic of the species groups and sometimes of individual species and varieties.

Whether the woody perennial or the herbaceous annual habit is primitive in Sclerocarpus is largely conjectural. The genus includes a woody perennial, herbaceous annuals, species which may be either annual or somewhat woody and perennial under favorable conditions, and annuals which live for one season but develop considerable secondary xylem in the stem. Generally, the herbaceous annual is believed to be derived from the woody perennial in the flowering plants, but in Sclerocarpus, the woody perennial condition may be secondarily derived, as Cronquist (1955) suggests is true in general for the Compositae.

The chromosome numbers found in Sclerocarpus suggest the derivation of three of the species groups from an ancestor with a haploid number of twelve. Sclerocarpus africanus, with a haploid number of eighteen, and the closely related S. phyllocephalus, could have been derived from an ancestor having the haploid number of twelve by the duplication of half the chromosome complement or, more likely, from a haploid number of six by triploidy. Species with a haploid number of eleven or fourteen could have been derived by aneuploidy from the ancestor with the haploid number of twelve. The reports by Turner, Powell, and King (1962), of haploid numbers of both eleven and twelve in Sclerocarpus uniserialis and S. divaricatus, if confirmed, would indicate a close relationship for these two species groups.

The four modern species groups in Sclerocarpus were probably derived from a distant common ancestor through a

number of intermediate forms. It is unlikely that any of the existing species closely resembles this supposed progenitor. The closely related Sclerocarpus africanus and S. phyllocephalus are probably recently derived from a common ancestral stock, Sclerocarpus sessilifolius appears to be an offshoot from a rather primitive form, while S. spatulatus, S. multifidus, and S. divaricatus have probably developed from a very recent common parent which had a haploid chromosome number of eleven, beakless sclerocarps and black-bearded disk corollas. Within this latter group, S. spatulatus probably most resembles the primitive form as its biseriate involucre of spatulate bracts most closely resembles the condition found in the other species groups. The most specialized species in this group is S. multifidus which is probably derived from S. divaricatus by the dissection of the leaves and other minor changes. The remaining two species of Sclerocarpus, S. papposus and S. uniserialis, may have been derived from plants with a haploid chromosome number of twelve and disk corollas with the peculiar torose trichomes in the beard which are common to both species. In S. papposus, in some respects most closely related to S. uniserialis var. uniserialis, reductions have occurred in the size of the receptacle, in the number of flowers, and in the size of the involucre bracts. The three varieties of S. uniserialis are very closely related and probably recently derived from a population with a wider distribution than that of any of the modern varieties. By differentiation and isolation, var. uniserialis may have

developed before or during migration into the geologically new coastal areas of southeastern Texas. Isolation of this variety apparently is involved with the geological development of the Rio Grande Valley. The other two varieties, var. frutescens and var. rubridiscus, developed by isolation from the parental population, possibly in relation to the mountain building in southern Mexico. It is problematical whether the complete isolation of the elements existed only in the northern part of the range, or whether isolation was once complete and has subsequently broken down in the south through adaptation and migration or under the influence of man. Whatever the history of the two varieties, there is at present, an incomplete isolation and introgression of the two varieties in Puebla and Oaxaca.

These morphological and cytological similarities and the inferred relationships are used in the construction of a diagram showing a possible evolution for the genus Sclerocarpus. (See Plate IV, fig. 2.) The four species groups are shown originating from a single source through a number of extinct intermediates. Both Sclerocarpus sessilifolius and the S. divaricatus group of species have black bearded disk corollas and presumably were derived from plants with this character. A haploid chromosome number of 12 is proposed for this ancestor as this number could be basic to all the modern species. Haploid numbers of 14 and 11 could readily be derived from it and one specimen of S. divaricatus has been reported to have a haploid number of 12, as reported elsewhere. The two

species in the S. uniserialis group are shown as derived from plants in which $n = 12$. These plants would have had the torose and reddish beard-trichomes which are found in both derived species and would not have been the immediate ancestor to S. sessilifolius and the S. divaricatus group as this would have had black beard-trichomes with smooth walls. Plants ancestral to all three groups might have had trichomes of simpler form and with reddish pigmentation. Black pigmentation in the S. sessilifolius-divaricatus line might have been a further development from this. The remaining two species, S. africanus and S. phyllocephalus, are shown diverging from a population in which the haploid number may have been 18, 12, or 6. These plants would probably have had unpigmented beard trichomes, and sclerocarps with complex tubercles, characters which are found in both species in the group. A plant with simple, unpigmented trichomes in the beard, sclerocarps with simple tubercles or none, and a haploid number of 6 could have been the progenitor of the whole genus.

This proposed evolutionary pattern is based on scanty evidence and is not presented as being accurate in detail but to indicate the general type of evolution which has apparently occurred in the genus. The determination of an evolutionary scheme by establishing an index of divergence is not satisfactory in the case of Sclerocarpus because of its few species with only a small number of characters separating them and the uncertain direction in which many of these have developed.

PLATE IV

Fig. 1. Morphology of trichomes from representative specimens of Aldama dentata. (a through g drawn from var. zamorensis, Feddema 1724, MICH; h through m drawn from var. dentata, Feddema 1541, MICH.)

A, stem, x 65; b, adaxial surface of leaf, x 65; c, d, e, abaxial surface of leaf, x 65; f, outer surface of disk corolla, below base of lobe, x 130; g, outer surface of disk corolla lobe, at apex, x 130; h, i, stem, x 65; j, abaxial surface of leaf, x 65; k, adaxial surface of leaf, x 65; l, m, outer surface of disk corolla, below base of lobe, x 130.

Fig. 2. Diagram suggesting possible evolutionary relationships in Sclerocarpus. Open circles represent extant taxa. Hatched circles represent putative extinct taxa. The numbers in the circles indicate numbers of chromosome pairs.

Plate IV

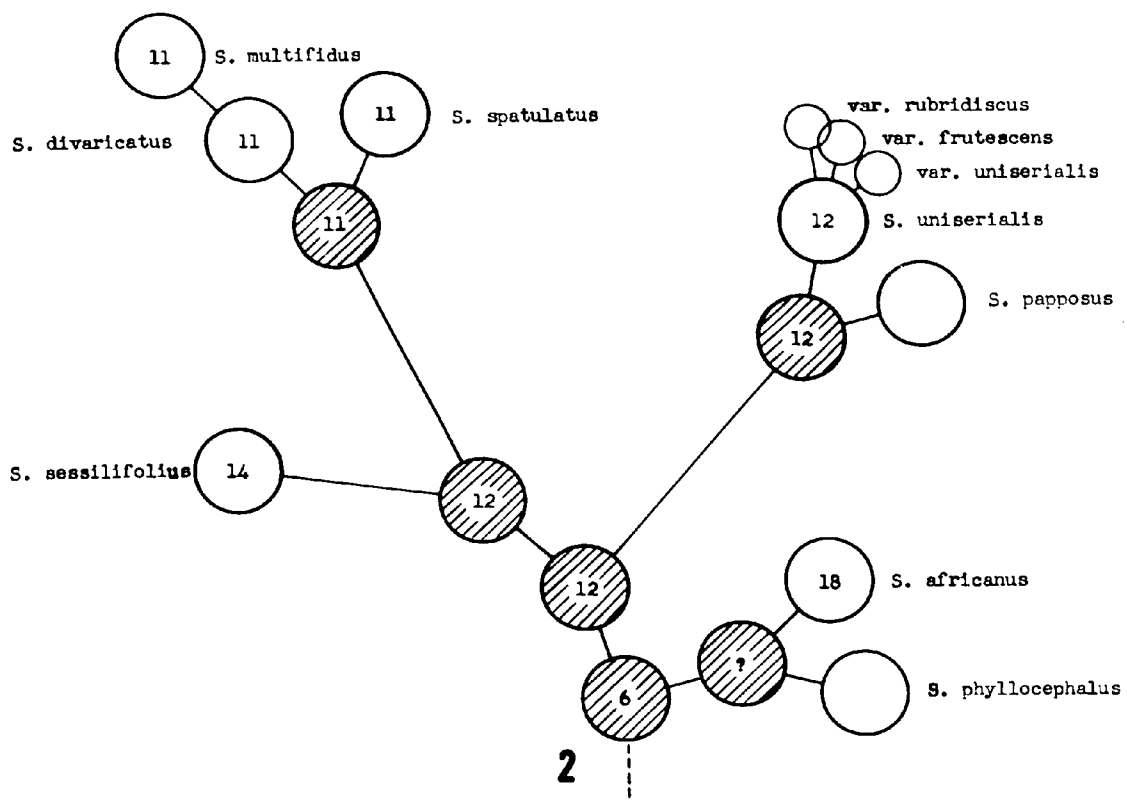
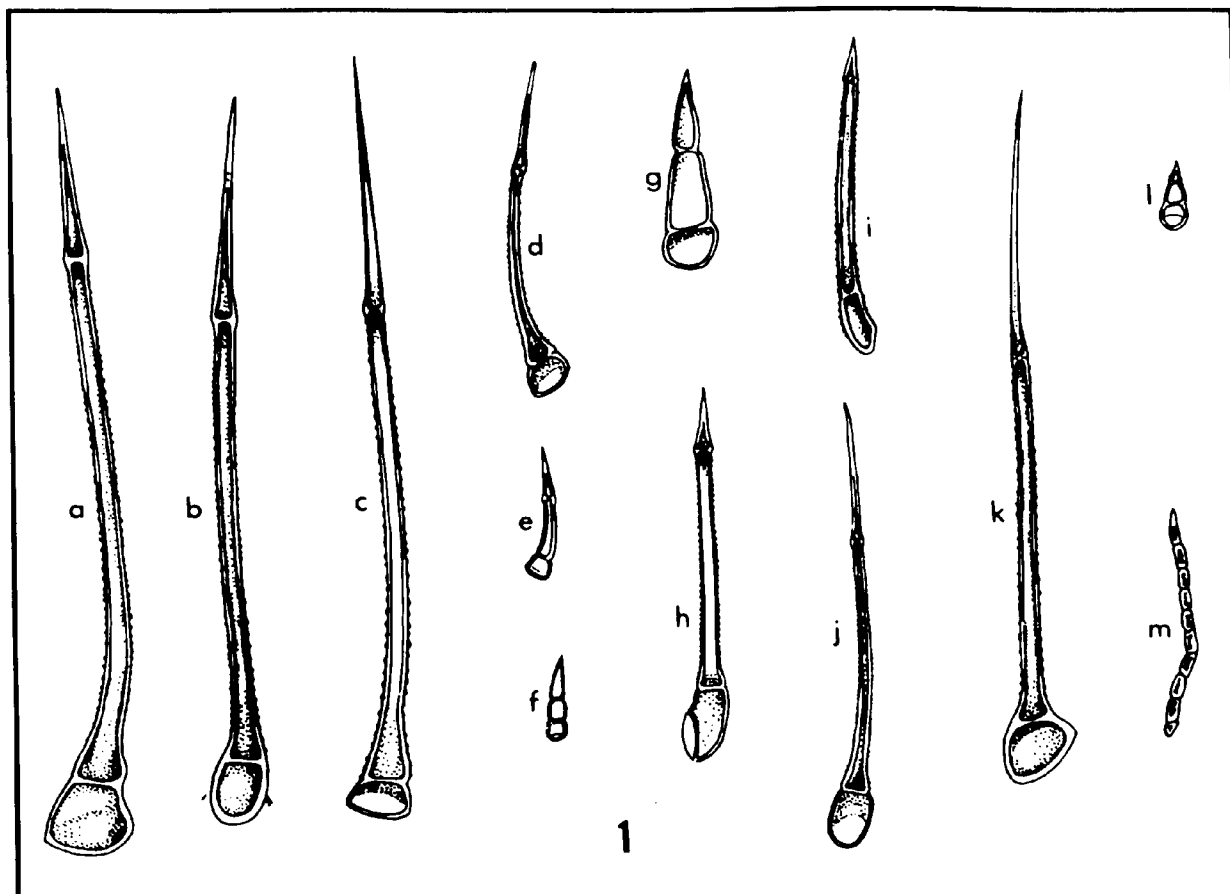


PLATE V

Distribution maps of Sclerocarpus divaricatus, S. papposus,
and S. africanus.

Plate V

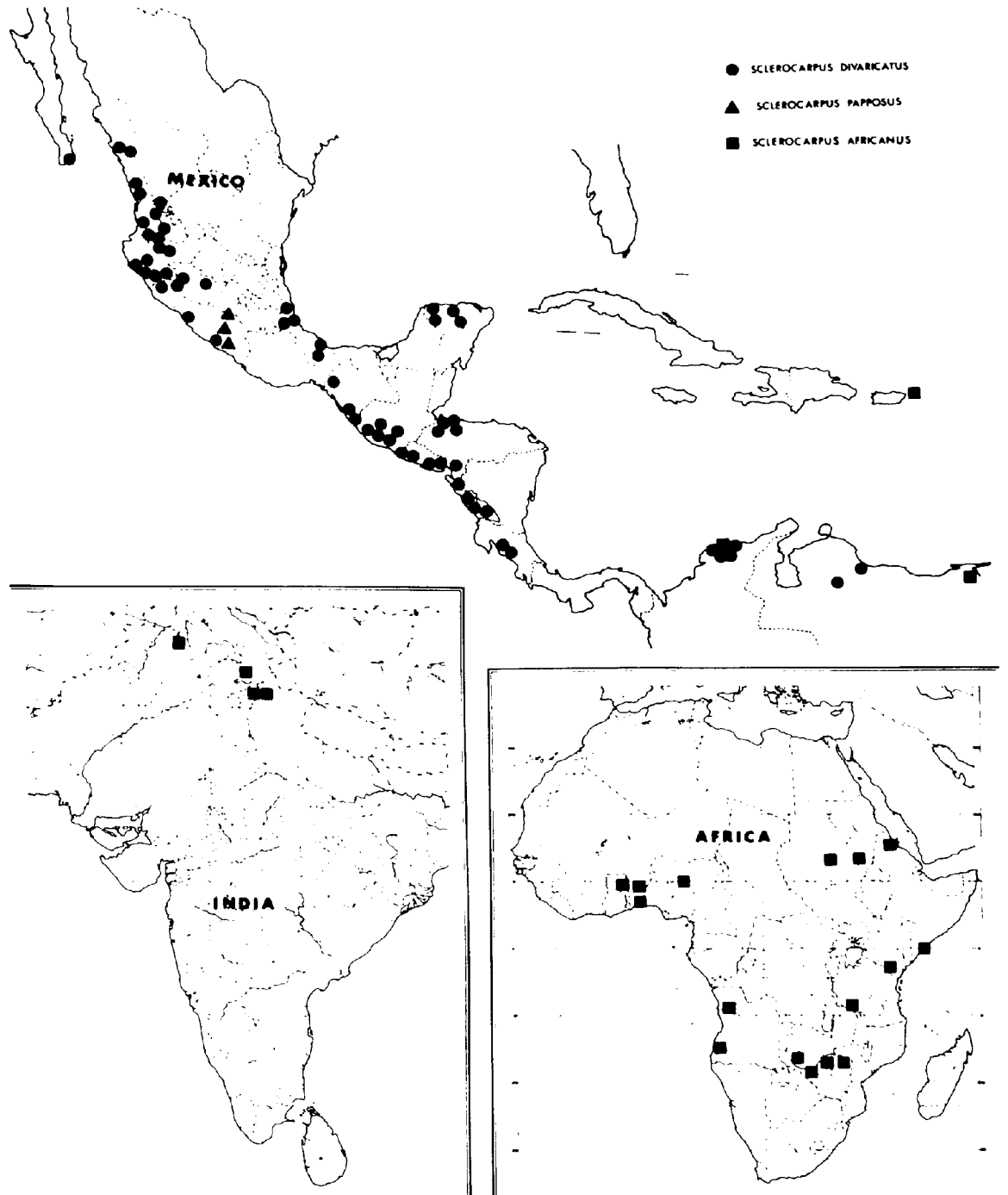


PLATE VI

Distribution maps of Sclerocarpus uniserialis, S.
spatulatus, S. sessilifolius, and S. multifidus.

Plate VI

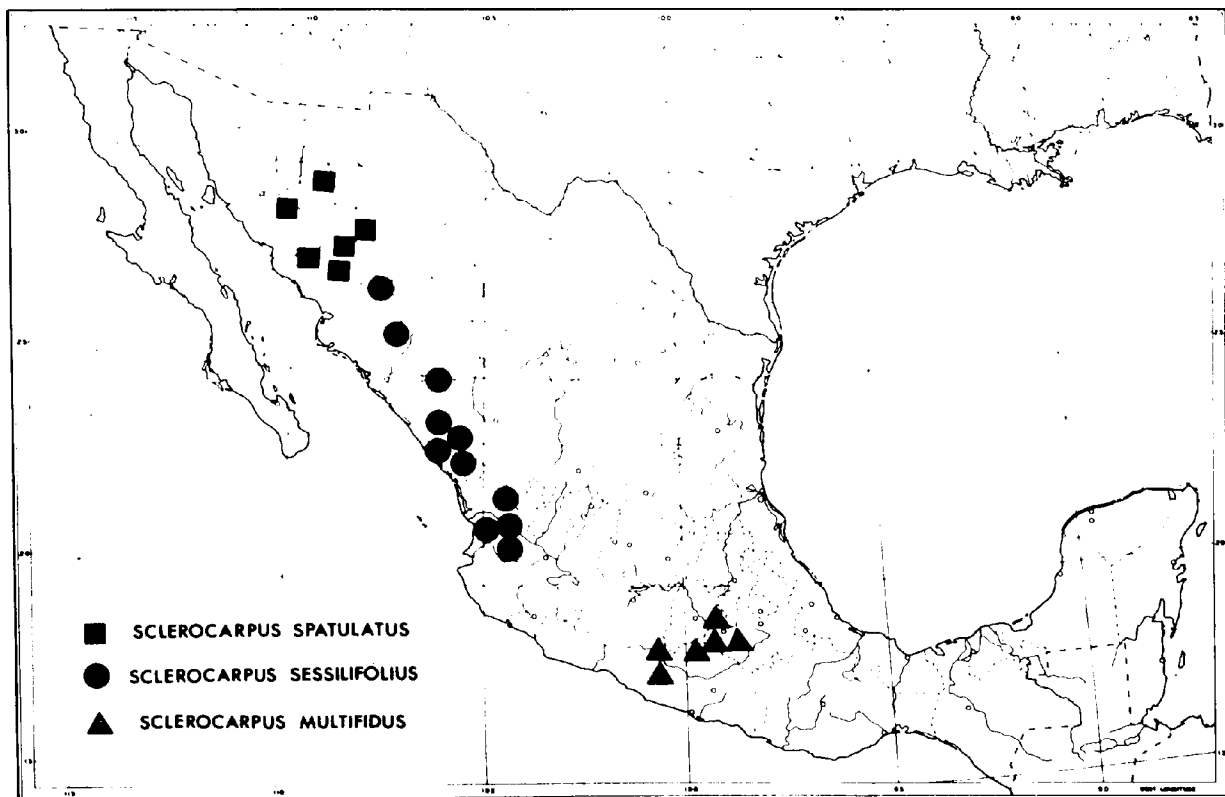
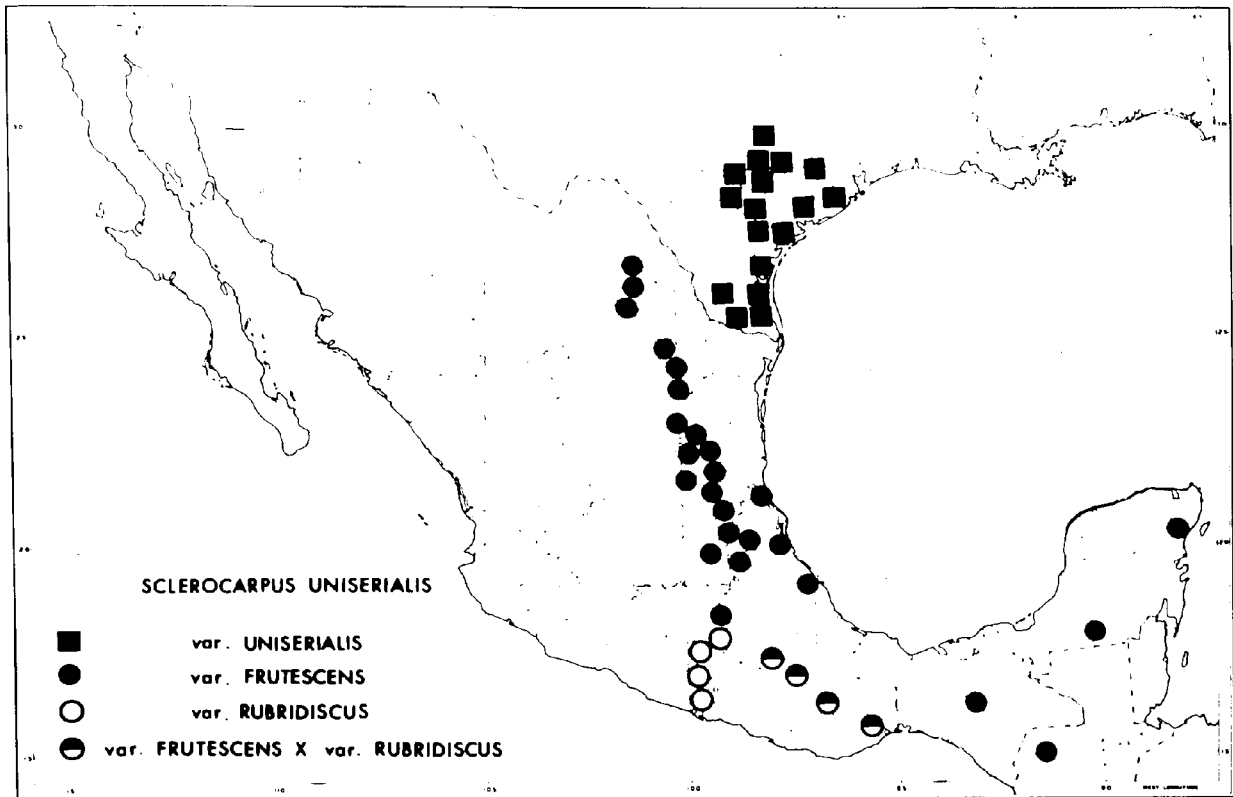
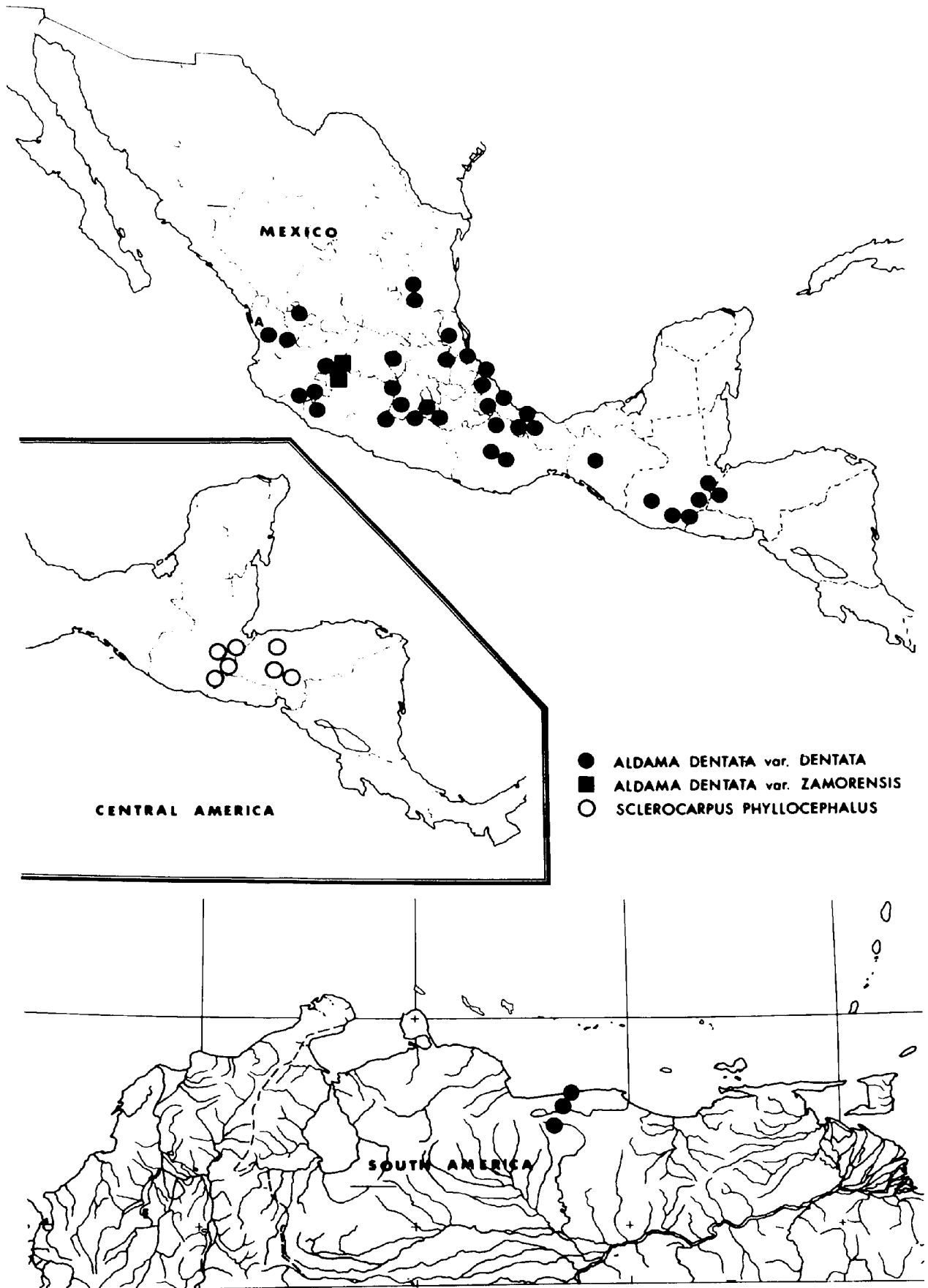


PLATE VII

Distribution maps of Sclerocarpus phyllocephalus and
Aldama dentata.

Plate VII



TAXONOMIC TREATMENT

SCLEROCARPUS Jacquin ex Murray, Syst. Veg. ed. 14. 783. 1784.

Mostly erect herbaceous annuals, rarely procumbent perennials, (0.1-) 0.3-1.3 (-2.5) m tall, usually well-branched; stem terete, green or reddish, the base sometimes woody in age, glabrate or with worn hair bases below, strigose or densely so with some spreading hairs above; lower branches opposite, long, decussate, procumbent or ascending; upper branches alternate; leaves three-nerved, the principal cauline ones long-petioled (except short-petioled in S. sessilifolius), dying on the maturing plant; leaves of the branches small, sometimes much reduced, those of the upper stem short-petioled; blades mostly 3-8 cm long, lanceolate, dark green and mostly scabrous-strigose adaxially, lighter green and more densely strigose with longer appressed hairs abaxially, the margin irregularly coarse dentate, occasionally serrate or shallowly so, rarely entire, the apex mostly acute, the base mostly cuneate and often decurrent on the petiole, the petiole sometimes very narrowly margined; heads one to very numerous, solitary, radiate, 5-23 mm high, mostly long-peduncled, terminal on the stem and branches; receptacle ovoid or conical, chaffy, mostly shallowly pitted; involucre uniseriate or biseriate, mostly campanulate in bud, rotate or reflexed in age with the maturing receptacular bracts exposed; involucral bracts 5-21, free, green, sub-foliaceous, one subtending each ray flower, or with additional bracts within or below on the involucre or

peduncle; ray flowers (3-) 5-9 (-16), neutral, ligulate, scarcely extending beyond the disk or spreading to a radius of 3.3 cm; ligules yellow or orange, ovate or subcircular, minutely strigulose abaxially, the apex 2-3 toothed; ray achenes fleshy or hollow, arcuate, trigonous, persisting on the receptacle and flattened or shriveled when dry; disk flowers 3-70, perfect, mostly 5-nerved, tubular, without a definite throat, 3.5-18 mm long, narrow at base, enlarging gradually to the lobes, the outer surface short pubescent; corolla lobes mostly 1.2-5 mm long, the apex spreading or reflexed, mostly short-pubescent outside, the inside short-papillate at apex and bearded above the middle of the lobe, the beard often black or dark, forming a conspicuous band around the corolla; anthers usually retained within the corolla tube, the base short-sagittate, the connective narrowly lanceolate-attenuate, 3-5 times longer than wide; stigmatic arms terete or slightly flattened, attenuate, the hairs outside mostly longest near the apex, decreasing in length and becoming merely papillate near the union of the arms or on the style; young receptacular bracts thin, green, tubular, loosely enclosing the ovule and base of the corolla; mature receptacular bracts of the marginal disk flowers much thickened and sclerified, each tightly enclosing an achene and its edges overlapping adaxially, the whole forming a flask-like structure here designated a sclerocarp; mature sclerocarps sometimes terminating at the apex of the achene which remains visible in the neck of the enclosing bract, or longer, then consisting of an

enlarged basal portion, or body, enclosing the achene, and a thin-walled apical portion, or beak, extending beyond and concealing the apex of the achene; body of the sclerocarp often somewhat laterally compressed, obliquely obovate in lateral outline, narrowed to the beak, the surface green, brownish, purplish black or mottled, glabrate or pubescent on the upper portion, striate or tubercled; beak of the sclerocarp often bent adaxially from the body, often pubescent; mature receptacular bracts enclosing the central disk flowers usually thin, chaffy, tubular, longer than those of the margin, loosely enclosing the achene, poorly differentiated into body and beak, the surface mostly glabrous, smooth or striate; achenes of the marginal sclerocarps usually black, shining, minutely striate, rarely dull gray, olivaceous or purplish brown, terete or somewhat laterally compressed, fusiform or obliquely obovate-turbinate in lateral outline, gradually narrowed to base; pappus an irregular tube or crown of fused bristles, a few irregular scales or none; achenes of the central disk flowers narrower and longer than those of the margin, frequently not developing; chromosome numbers $n = 11, 12, 14, 18$. Type species: Sclerocarpus africanus Jacquin ex Murray.

The generic name Sclerocarpus was first published by Nikolaus Joseph von Jacquin (1781) in the first volume of his Icones Plantarum Rariorum, in which plate 176 bears the title Sclerocarpus africanus. This three volume work contains colored plates of plants which were growing in the

botanic garden of Vienna or the Imperial garden of Schönbrunn (cf. Stearn, 1961). Murray (1784), in the fourteenth edition of Linnaeus' Systema Vegetabilium, included a brief description of the genus Sclerocarpus and the species Sclerocarpus africanus. Jacquin (1787) then published a more complete description of the genus and species in a paper entitled Tria genera plantarum nova, which appeared in the first volume of the Nova Acta Helvetica (often incorrectly cited as volume nine of the Acta Helvetica, a projected volume which never appeared as such). Murray, who was apparently in communication with Jacquin, had attributed authorship of the genus to the latter, citing the unpublished ninth volume of the Acta Helvetica and citing the species as from the Icones Plantarum Rariorum. Curiously, Jacquin in the Icones had cited Murray's edition of the Systema Vegetabilium and volume nine of the Acta Helvetica, both of which were still unpublished in 1782. Although most authors have credited the genus and species to Jacquin and have cited both the Icones and the Acta Helvetica, Blake (1930) correctly indicated that the plate in the Icones is only a habit sketch and that according to the rules of nomenclature, the genus Sclerocarpus and the species Sclerocarpus africanus must properly be cited from the fourteenth edition of the Systema Vegetabilium of Murray.

KEY TO THE SPECIES OF SCLEROCARPUS

Leaves strongly dissected or pinnatifid; ligule orange with
 bright yellow teeth. Morelos and Guerrero.....
1. S. multifidus p. 56

Leaves toothed, rarely entire; ligule and its teeth of the
 same color.

Mature marginal sclerocarps beakless, or terminating in
 a low rim or collar, the achene visible in the neck of
 the bract; base of the marginal disk achenes strongly
 curved upward.

Involucral bracts 5-7, in one series, ovate, oblong,
 obovate or broadly lanceolate. Mexico, Central
 America and northern South America.....
2. S. divaricatus p. 62

Involucral bracts more than 10, in two series, linear-
 spatulate or oblanceolate. Sonora and southwestern
 Chihuahua.....3. S. spatulatus p. 75

Mature marginal sclerocarps with a tubular beak con-
 cealing the apex of the achene; base of the marginal
 disk achenes straight or only slightly curved.

Involucral bracts inconspicuous, mostly minute,
 acicular, less than 3 mm long; receptacle conspicu-
 ously white-pubescent at maturity; pappus of the
 mature marginal disk achenes 1.5-4 mm long; anthers
 conspicuously exserted from the corolla at anthesis.
 Eastern 4. S. papposus p. 81

Involucral bracts conspicuous, blade-like, mostly more than 3 mm long; receptacle glabrous or with a few hairs or scales at maturity; pappus of the marginal disk achenes less than 1.5 mm long; anthers rarely somewhat exserted from the corolla at anthesis.

Principal cauline leaves subsessile or short-petioled, the petioles $1/6$ - $1/10$ as long as the blade; lobes of the disk corolla with black hairs inside; base of the stem with an irregular or rounded woody tuber; mature stem procumbent or ascending. Nayarit, Sinaloa, western Durango.....
5. S. sessilifolius p. 86

Principal cauline leaves long-petioled, the petioles more than $1/6$ as long as the blade; lobes of the disk corolla with hyaline, yellow or purple red hairs; base of the stem unthickened or cylindrically or conically thickened; mature stems mostly erect, rarely ascending.

Ray achenes hollow when living, thin and flattened when dry, pubescent on the angles; receptacle less than $1-1/2$ times as long as wide; mature outer involucral bracts often similar in form and size to the upper leaves.

Beak of the mature marginal sclerocarp less than $1/3$ as long as the body, the body **more than 4.7** mm long, sharply reduced to the beak, the ad-axial surface with numerous low, angulate tubercles or ridges. St. Thomas (American Virgin Islands), northern Colombia, northeastern Venezuela, Tropical Africa, West Pakistan and northern India.....6. S. africanus p. 93

Beak of the mature marginal sclerocarp $1/2$ to nearly as long as the body, the body **less than 4.7** mm long, gradually reduced to the beak, the abaxial surface with a few conspicuous, long, contorted or flattened tubercles. Guatemala, Honduras, and Nicaragua.....

7. S. phyllocephalus p. 101

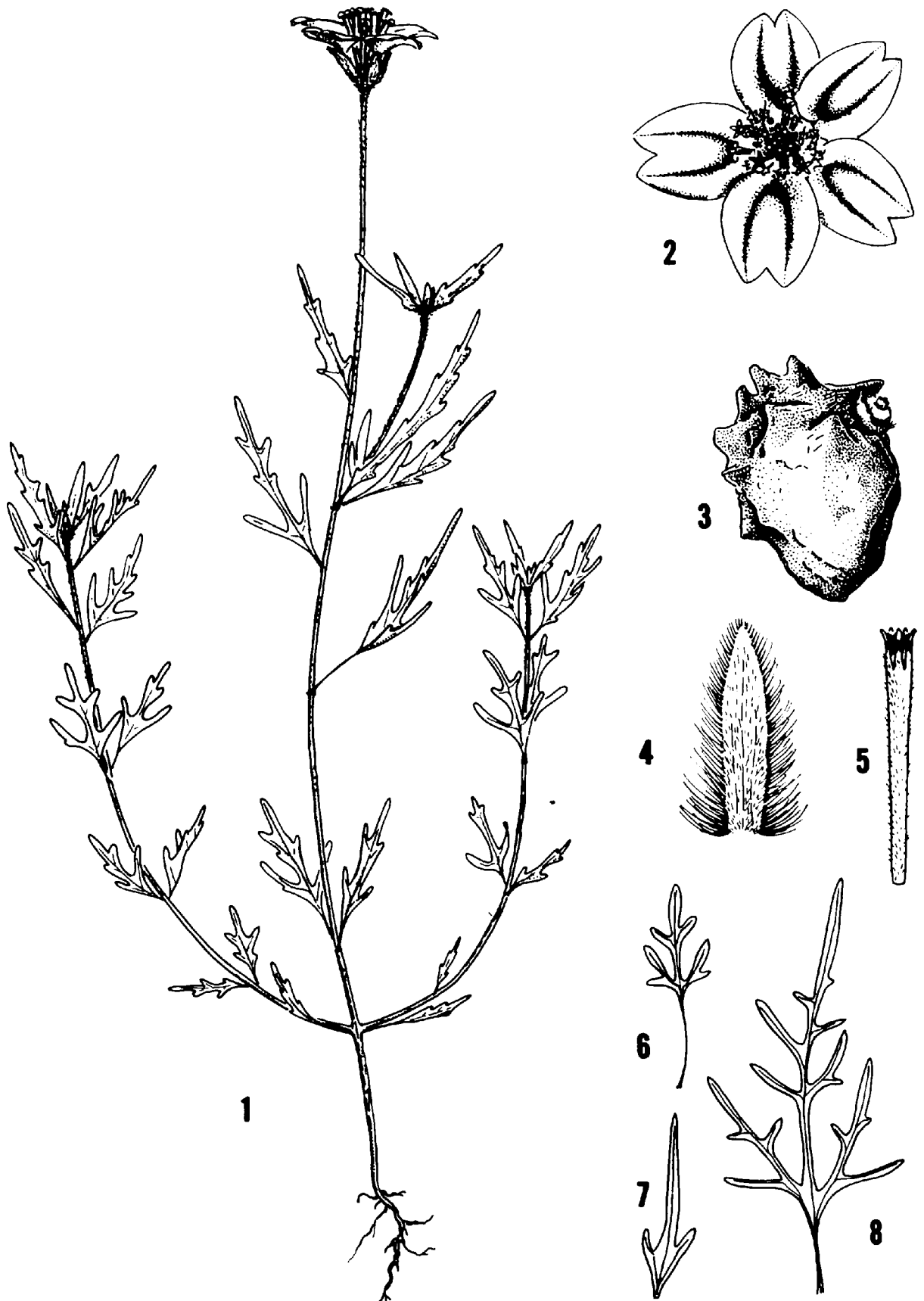
Ray achenes fleshy throughout when living, shriveled and twisted when dry, glabrous; receptacle more than $1-1/2$ times as long as wide; mature outer involucre bracts greatly modified in form and reduced in size compared to the upper leaves. Texas, eastern and southern Mexico and Guatemala.....

.....8. S. uniserialis p. 108

PLATE VIII

SCLEROCARPUS MULTIFIDUS Greenman

- Fig. 1. Habit sketch, x 0.7, G. B. Hinton 9187 (MICH).
- Fig. 2. Capitulum, viewed from above, x 1.5, Feddema 1644 (MICH).
- Fig. 3. Mature marginal sclerocarp, lateral view, x 15, Feddema 1621 (MICH).
- Fig. 4. Involucral bract, abaxial surface, x 3.5, Feddema 1664 (MICH).
- Fig. 5. Disk corolla, x 5, Feddema 1621 (MICH).
- Fig. 6. Lower cauline leaf from young plant, x 0.7, Feddema 1664 (MICH).
- Fig. 7. Leafy bract from base of peduncle, x 0.7, Feddema 1664 (MICH).
- Fig. 8. Mature cauline leaf from robust plant, x 0.7, Feddema 1664 (MICH).



1. *SCLEROCARPUS MULTIFIDUS* Greenman, Field Mus. Publ. Bot.
2:346. 1912. Plate VIII.

Erect annual, (1-) 3-4 (-10) dm tall, with a short, unbranched, slender stem (in impoverished specimens), or much-branched, nearly subglobose in robust individuals; stem with tufts of spreading, multi-celled hairs to 2 mm long at the base of the petioles; younger branches and peduncles densely pubescent with subappressed or spreading hairs to 1.5 mm long; leaves (2-) 3-5 (-10.5) cm long, including the petioles, the lower long-petiolate, the uppermost short-petiolate or sessile; petioles mostly $1/3$ - $1/2$ as long as the blade; blades ovate-lanceolate, 2-5 (-9) cm long, (0.5-) 1-3 (-5) cm wide, mostly deeply pinnatifid with 3-8 linear segments, these opposite at the base of the blade, alternate near the apex, the longer ones narrowed at base, the basal ones sometimes again pinnately lobed; base of the blade cuneate, narrowly decurrent on the petiole; adaxial surface of the blade with whitish bulbous-based hairs 0.2-1.0 mm long, these rarely yellowish on very young leaves; heads one to few, rarely numerous, 11-18 mm high, on peduncles to 15 cm long; peduncles naked, rarely with a few reduced leafy bracts; receptacle ovoid, 2-4 mm long, 2-3.7 mm diameter, the apex rounded, the pits with raised hispidulous margins; involucre uniseriate, campanulate, 6-12 mm diameter when young, becoming subrotate, when achenes mature; involucral bracts 5, narrowly lanceolate, elliptic, or rarely narrowly ovate, the margin ciliate, the abaxial surface with

appressed hairs 0.3-1 mm long above the middle and with spreading, multi-celled hairs to 2.5 mm long at base; ray flowers 5(-6), 11-15 mm long, including the tube, spreading radially to 18 mm from the center of the disk; ligules orange, 6-11 mm long, 7-12 mm wide, broadly ovate or sub-circular, nearly perpendicular to the tube, with 2(-3) longitudinal grooves adaxially, terminating in yellow-tipped teeth to 2.5 mm long, the abaxial surface sparsely strigulose with orange hairs 0.3-0.7 mm long; tube of the ray corolla 2.5-5 mm long; achenes of the ray flowers 2-4 mm long, greenish or white, arcuate, fleshy when living, the body often shriveled and twisted when dry; disk flowers 10-34, oriented in the head nearly parallel to the axis of the receptacle; disk corollas 9-18 mm long, the inner surface short yellow-papillate at apex and with a beard of blackish hairs below, these projecting beyond the margins of the lobes and visible as a black band around the corolla near the middle of the lobes; mature marginal receptacular bracts usually fused at edges basally, the sclerocarp somewhat laterally compressed, obliquely obovate in lateral outline, 3-4.5 mm long, the apex of the sclerocarp forming a low ciliate rim, this sometimes with an adaxial tooth which may be long or blade-like on inner sclerocarps; surface of the sclerocarp green, brownish, purplish or mottled, usually black, with appressed or erect hairs and conical tubercles on the abaxial ridge and laterally toward the apex; bracts of the central disk graduate, those of the inner 2-3 rows to 8 mm long, only

slightly thickened, whitish or light colored at base, extending beyond the achene in a trough-like blade, this orange and ciliate distally, the abaxial surface with orange hairs above the middle; achenes of the marginal 2-3 rows of disk flowers obliquely obovoid, nearly terete, 2.5-3.5 mm long, 1.4-2 mm measured radially, the base whitish, narrowed and recurved upward, the apex crowned with a short cylinder, the pappus a low yellowish ring, or none; chromosome number, $n = 11$ (Feddema 1621, MICH).

Mexico, Morelos and Guerrero, at elevations of 450 to 1950 meters, flowering July to September.

Type: GUERRERO: Río Balsas, 26 Aug, 1910, C. R. Orcutt 4177 (Holotype F!; isotypes GH! US! MO!).

This species is most closely related to S. divaricatus from which it differs chiefly in having pinnatifid leaves. It also is generally shorter, and has an orange ligule with yellow-tipped teeth.

Specimens examined:

MEXICO: District of Temascaltepec, Anonas, 23 Aug 1933, G. B. Hinton 4573 (A, K, MICH, MO, NY, US).

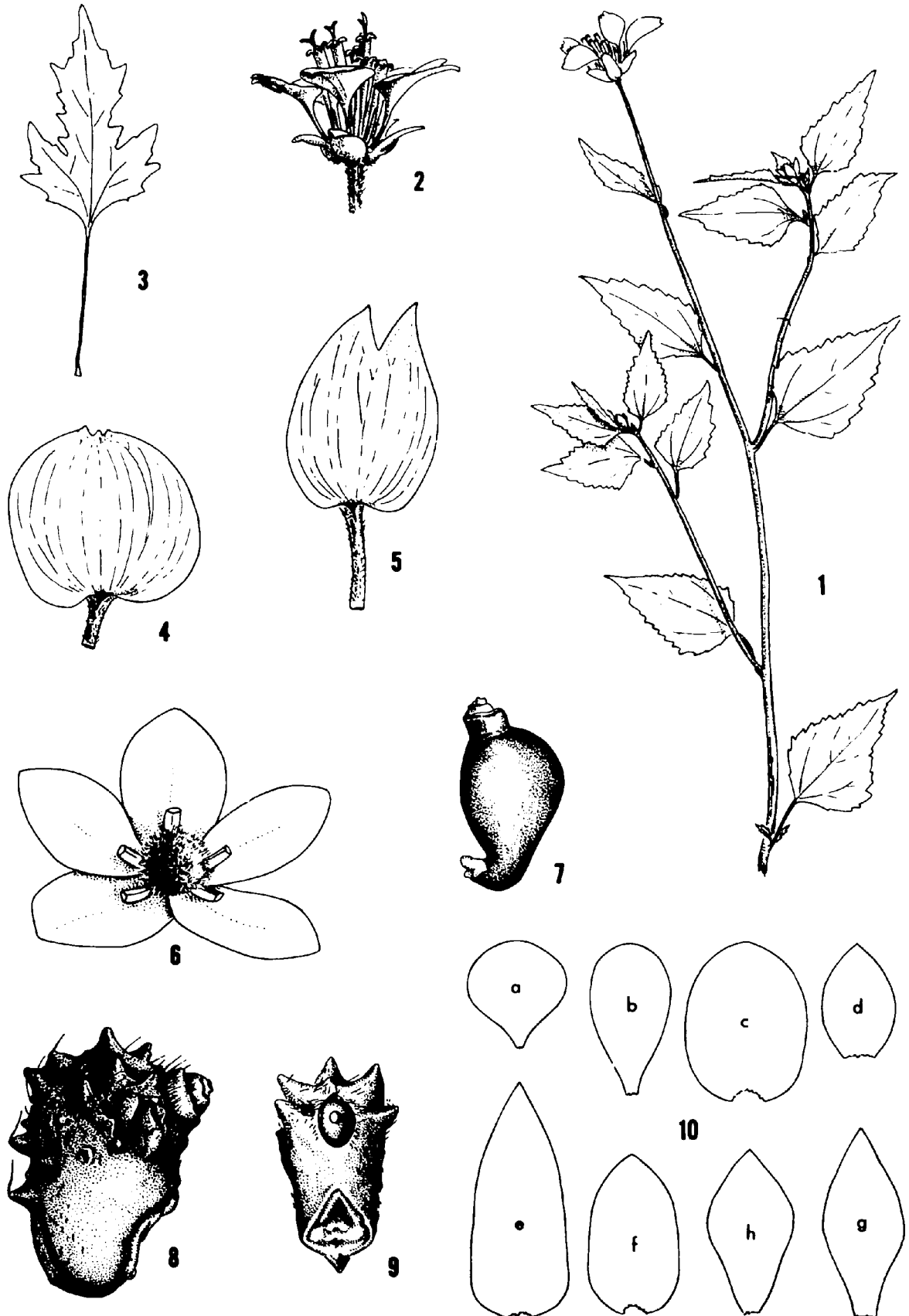
MORELOS: 12 km NW of Axochiapán, 10 Aug 1950, G. P. Nye 6 (MICH); 2 km S of Cuernavaca, 11 Aug 1961, Feddema 1612 (MICH); 6 km S of Cuernavaca, 11 Aug 1961, Feddema 1613 (MICH); near Amacuzac, 12 Aug 1961, Feddema 1621 (MICH); 6 km S of Amacuzac, 13 Aug 1961, Feddema 1664 (MICH); 25 mi N of Taxco, Guerrero, 21 Aug 1947, Rowell, Paxson & Barkley 17M929 (TEX).

GUERRERO: District of Mina, Placeres-Camérón, 1 Aug 1936, Hinton 9187 (GH, MICH, US); District of Mina, Manchón, 1 Sep 1936, Hinton 9419 (MICH, GH, TEX); Taxco, 23 Aug 1940, Kenoyer C400 (GH); District of Coyuca, Cutzamala, 11 Aug 1934, Hinton 6425 (A, K, MO, NY, US); District of Coyuca, Chacamérito, 9 Aug 1935, Hinton 8150 (GH, NY, US).

PLATE IX

SCLEROCARPUS DIVARICATUS (Benth.) Benth. & Hook. f. ex
Hemsl.

- Fig. 1. Upper branch, x 0.5, Feddema 1555 (MICH).
- Fig. 2. Young capitulum, x 1, Feddema 1555 (MICH). (From photograph.)
- Fig. 3. Leaf, showing lobing (possibly due to introgression with S. multifidus), x 0.5, McVaugh 18557 (MICH).
- Fig. 4. Common type of ray corolla, x 2.5, Feddema 1730 (MICH).
- Fig. 5. Elongate type of ray corolla, x 2.5, Feddema 1570 (MICH).
- Fig. 6. Receptacle after the fall of the receptacular bracts and achenes, x 2.5, Feddema 1555 (MICH).
- Fig. 7. Marginal disk achene with enclosing bract removed, lateral view, x 10, Feddema 1570 (MICH).
- Fig. 8. Receptacular bract enclosing the marginal disk achene, lateral view, x 12, Feddema 1580 (MICH).
- Fig. 9. Receptacular bract enclosing the marginal disk achene, adaxial view, x 10, Feddema 1621 (MICH).
- Fig. 10. Diagram showing variation in form of involucral bracts, x 2.5. a, Rose 3477 (US); b, Palmer 975 (US); c,d,e,f, Feddema 1580 (MICH); g, Feddema 1727 (MICH); h, Feddema 1730 (MICH).



2. *SCLEROCARPUS DIVARICATUS* (Benth.) Benth. & Hook. f. ex
Hemsl., Biol. Centr. Am. Bot. 2:164. 1881. Plate IX.

Gymnopsis divaricata Benth. Bot. Voy. Sulph. 116. 1845.

Type: Gulf of Fonseca, Sinclair (Holotype K!).

Sclerocarpus orcuttii Greenm. Field Mus. Publ. Bot. 2:346.
1912.

Type: COLIMA: Colima, 24 Oct 1910, C. R. Orcutt 4599
(Holotype F!; isotypes MO! GH!).

Sclerocarpus triunfonis M. E. Jones, Extracts from Contr.

West. Bot. 18:77. 1933. Type: BAJA CALIFORNIA: Triunfo,
6 Oct 1930, M. E. Jones 27717 (Holotype POM.).

Erect annual, (1-) 5-10 (-17) dm tall, usually well-branched (short, slender and unbranched in impoverished specimens), glabrate or sparingly short-strigose below, more densely pubescent on young portions of branches and peduncles with longer, appressed or somewhat spreading hairs, rarely with erect or spreading multi-celled hairs to 3 mm long; leaves, including the petioles, (2-) 3-9 (-15) cm long, the lower large with petioles 1/2 to nearly as long as the blade, the upper smaller with petioles mostly 1/5 to 1/2 as long as the blade; blades (2-) 3-5 (-11) cm long, (0.5-) 1.3-3.5 (-7) cm wide, narrowly to broadly ovate-trullate, rarely ovate-deltoid; margin of the blade dentate or crenate with (2-) 5-9 (-16) uniform or irregular sharp or rounded teeth on each side, rarely with irregularly toothed lobes at base; base of the blade cuneate, narrowly decurrent on the petiole, the apex acute or acuminate, the tip sometimes rounded, the abaxial surface with coarse

whitish hairs to 1 mm long; heads one to several, 8-18 mm high, on peduncles to 15 cm long; peduncles naked or with one, rarely more, reduced leafy bracts; receptacle broadly ovoid conoid, 2-4 mm diameter, 1-3 mm long (to 7 mm diameter, 6 mm long when living), the apex rounded, the pits with raised hispidulous margins; involucre uniseriate, campanulate, 7-18 mm diameter when young, becoming enlarged and rotate as achenes mature; involucre bracts 5 (-6), rarely more, 5-15 mm long, (2-) 3-6 (-8) mm wide, each subtending a ray achene, ovate-lanceolate, oblong or obovate, the apex acute or obtuse, rarely rounded, the base broadly rounded, cordate or sharply narrowed; surface of the involucre bract mostly strigose adaxially or scabrous toward the tip, strigose or substrigose abaxially with hairs to 0.8 mm long, these spreading at base of the bract; ray flowers 5 (-6), very rarely to 9, (8-) 15-23 mm long including the tube, spreading radially to 2.3 cm from the center of the disk; ligules yellow orange, narrowly to broadly ovate or sub-circular, (5-) 8-16 mm long, 6-15 mm wide, nearly perpendicular to the tube, with teeth (0.3-) 0.5-2.0 (-3) mm long, sparsely strigulose abaxially with yellow hairs to 0.7 mm long, rarely with additional black hairs less than 0.1 mm long; tube of the ray corolla mostly $1/3-1/2$ as long as the ligule with hairs to 0.7 mm long; achenes of the ray flowers 1-3 mm long, green or whitish, fleshy when living, the body often shriveled when dry; disk flowers (12-) 25-45 (-60), oriented in the head nearly parallel to the axis of the receptacle; disk corollas slender, 8-17 mm long, 0.3-0.7 mm

diameter at base, 0.8-1.7 mm diameter at the lobes, the outer surface short pubescent at base of the tube and with stiff orange hairs to 0.7 mm long on the lobes; corolla lobes 2-4 mm long, the inner surface short yellow-papillate at the apex and with a beard of blackish hairs below, these projecting beyond the margins of the lobes and visible as a black band around the corolla near the middle of the lobes; mature sclerocarps of the marginal 2-3 rows of disk flowers somewhat laterally compressed, obliquely obovate in lateral outline, 2.7-4.5 mm long, 1.8-2.5 mm measured radially, the apex of the sclerocarp forming a low ciliate rim around the apex of the achene, the rim sometimes with an abaxial tooth which may be long or blade-like on inner sclerocarps; surface of the sclerocarps green, brownish, purple or mottled, usually blackish when mature, sparsely strigose-hispidulous with conical tubercles on the abaxial ridge and laterally toward the apex; receptacular bracts of the central disk graduate, those of the innermost rows to 8 mm long, somewhat thickened at base, extending beyond the achene in a yellowish or straw-colored blade, this sparsely strigose abaxially and with yellowish cilia at the apex and distal margin; achenes of the marginal 2-3 rows of disk flowers somewhat laterally compressed or nearly terete, obliquely obovate in lateral outline, 2.5-4 mm long, 1.5-2.3 mm measured radially, the base whitish, narrowed and recurved upward, the pappus absent or rarely suggested by a low rim, minute bristles or scales; chromosome number $n = 11$ (Feddema 1555, MICH).

Western Mexico from Baja California and Sinaloa to Guerrero, eastern Mexico from Veracruz to Yucatan and Chiapas, Central American from Guatemala to Costa Rica, the region near Barranquilla in Colombia and the region near Caracas in Venezuela, at elevations from sea level to 1500 meters, flowering from July to November in northwest Mexico, persisting until February or March in Colima, Vera Cruz and Yucatan, and found in flower throughout most of the year except for local dry seasons throughout the rest of its range.

This widespread species is most closely related to S. spatulatus and S. multifidus. It shows considerable variation in the form of the involucre bracts. A study of this variation indicates the presence of two, more or less distinct races. In specimens from western Mexico from Baja California and Sonora to Colima, the involucre bracts are generally obovate and narrow at base. In those from eastern Mexico, Central America and South America, the involucre bracts are mostly broadly ovate-lanceolate and widest near the base. Because of the somewhat minor nature of this single character and because of the variation found among the bracts of a single head, it is not deemed advisable to accord formal taxonomic recognition to these populations.

The type location of Sinclair's collection is, "The Gulf of Fonseca", which is bounded by El Salvador, Honduras, and Nicaragua. The type of Sclerocarpus triumfonis M. E. Jones was regarded by S. F. Blake (1945), as a synonym of S. divaricatus.

Specimens examined:

BAJA CALIFORNIA: Cape St. Lucas & c., Aug 1859- Jan 1860, L. J. Xantus 59 (GH, NY, US); San José del Cabo, 1899, T. S. Brandeggee (GH); Corral Piedra (Cape Region), 10 Sep 1893, Brandeggee (NY).

SINALOA: Imala, 29 Nov 1939, H. S. Gentry 5086 (GH, MICH, MO, NY); Mocorito, 27 Sep 1923, Collins & Kempton 63 (US); El Norote, 1925, J. G. Ortega 5918 (US); Ymala [Imala], 25 Sep - 8 Oct 1891, E. Palmer (US); Santa Mariá, Baila, Culiacán, Jul 1934, Ortega 6723 (US, MO); El Monte, Los Labrados [Labradas], 15 Oct 1926, Ynes Mexia 932, (F, GH, MICH, MO, US, NY); La Noria Foothills, 7 Oct 1925, Mexia 118 (MO).

DURANGO: Huazamota, 14 Aug 1897, J. N. Rose 3477 (US).

NAYARIT: above La Laguna, near Santa María del Oro, 4 Oct 1962, A. Cronquist 9596 (NY, TEX); cañon de Jesús María, 31 Aug 1905, P. Goldsmith 151 (GH); 48 km E of San Blas, 20 Aug 1961, Feddema 1775 (MICH); Tetitlán, 15 Aug 1959, Feddema 492 (MICH); 6 km E of Ixtlán del Río, Feddema 1730, 11 mi NW of Ixtlán del Río, 10 Aug 1960, R. M. King 3679 (MICH, TEX).

JALISCO: Bolaños, 10-19 Sep 1897, J. N. Rose 2872 (GH, US); 15 km E of Plan de Barrancas, 19 Aug 1961, Feddema 1730 (MICH); 25 mi W of Tequila, 24 Aug 1961, Powell & Edmondson 878 (MICH, TEX); Tequila, 28 Sep 1893, C. G. Pringle 4607 (F, GH, MICH, NY, TEX, US); barranca of the Rio Grande, N. of Amatitlán, 1 Sep 1960, R. McVaugh 18557 (MICH); Guadalajara, Sep 1886, Palmer 415 (GH, NY);

Guadalajara, Jul-Oct 1886, Palmer 147 (US); 10 km N of Puerto Vallarta, 16 Nov 1963, Feddema 1601 (MICH); 11 mi S of Autlán, 8 Aug 1949, R. L. & C. R. Wilbur 2194 (MICH, US); 4 mi N of Bahía de Navidad, 8 Nov 1960, McVaugh 20835 (MICH); 10 km NE of Tamazula, 16 Aug 1961, Feddema 1727 (MICH); Calabazas, 1925, B. P. Reko (US); approx. 15 mi NW of Tepalcatepec, Michoacán, 26 Oct 1963, Feddema 2242 (MICH).

COLIMA: Manzanillo, Dec 1890, Palmer 975 (GH, NY); 1 km W of Colima, 13 Mar 1943, Gilly, Bonisteel & Dodds 43 (MICH); Colima, Aug 1897, Palmer 114 (MICH, US); Colima, 9 Jan - 6 Feb 1891, Palmer 975 (US); Colima, without other locality, 9 Jan - Feb 1891, Palmer 1 (GH, NY, US); 16 km E of Colima, 16 Aug 1961, Feddema 1728 (MICH).

MICHOACAN: Aguililla, distr. Apatzingán, 13 Sep 1939, G. B. Hinton 15165 (K, MICH, NY, US); Tepalcatepec, Distr. Apatzingán, 24 Aug 1939, Hinton 12091 (GH, MICH, TEX, US); Coalcomán, 25 Aug 1939, Hinton 15139 (GH, NY, TEX, US); Coalcomán, 16 Mar 1939, Hinton 13658 (GH, MO, NY, TEX, US); El Calabazal [Talabasal], 14 Oct 1898, Langlasse 447 (GH, K, MICH, US); below Acahuato, Tancitaro region, Munic. Apatzingán, 14 Aug 1941, Leavenworth & Hoogstraal 1528 1522 (F); 15 Aug 1941, Leavenworth & Hoogstraal 1575 (F, GH, MO); Morelia, Sep 1900? Bro. Arsene (F).

GUERRERO: Acapulco and vicin., Oct 1894 - Mar 1895, Palmer 19 (GH, MO, US); between Acapulco and Pie de la Cuesta, 24 Aug 1935, L. H. MacDaniels 230 (F); 6 mi N of Acapulco, 20 Aug 1947, Barkley, Paxson & Westlund 17[?] (TEX).

VERACRUZ: Jalapa, Jan 1894, C. L. Smith 1741, specimen I, (GH); Zacuapán, Mar 1930, C. A. Purpus 15031 (F, GH); Zacuapám [Zacuapán] Oct 1929, Purpus 14055 (F, US); Barranca panoaya, Oct 1920, Purpus 8575 (GH, MO, NY, US); 30 km SE of Córdoba on the highway to Veracruz, 5 Aug 1961, Feddema 1555 (MICH); San Francisco, near Veracruz, 1894, C. L. Smith 1384 (NY); 37 km SE of San Andrés, 6 Aug 1961, Feddema 1570 (MICH); near los Mangos, SE of Catemaco, 19 Aug 1953, Dressler & Jones 123 (F, GH, US); 20 mi S of Acayucán, 8 Jun 1960, King 2733 (MICH, NY, TEX, US).

YUCATAN: Muna, 22-23 Jul 1932, W. C. Steere 2178 (MICH); Uxmal, 20-21 Jul 1932, Steere 2004 (MICH); Peto, 26-27 Jul 1932, Steere 2333 (MICH, US); near Izamal, Geo. F. Gaumer 771 (F, GH, MICH, MO, NY, US); Gaumer 410 (NY), Gaumer 1950 (F, GH, MO, NY, US); Gaumer 1489 (F, GH, NY); Temax, Gaumer 2503 (F, GH, NY); Uxmal, 29 Sep 1959, O. Degener 26769 (MO); Isimna [?] near Merida, 14 Mar 1903, Ed. Sellar 3939 (F).

OAXACA: woods near the Pacific, Cordillera, Nov - Apr 1840, H. Galeotti 2062 (K).

CHIAPAS: 16 km NE of Las Cruces, 7 Aug 1961, Feddema 1580 (MICH); 5 mi NE of Las Cruces, 22 Jul 1960, King 3440 (MICH, NY, TEX, US); Soconusco, [Socunusco] along railroad track to Tapachula, 29 Jun 1960, King 3126 (MICH, NY, TEX, US); Tapachula, 6 Aug 1936, G. L. Fisher 35200 (US); Tapachula, 6 Aug 1935, Fisher 35275 (F, MO); Aguas Calientes, Escuintla, 4 May 1948, E. Matuda 17772 (F, NY); Belén, Mapastepec, 14 Jul 1947, Matuda 16748 (F).

GUATEMALA: Río Vil, W of Retalhuleu, Dept. Retalhuleu, 24 Feb 1941, P. C. Standley 88295 (F); Retalhuleu, Mar 1871, Bernoulli & Cario 1295 (K); Río Samalá, Dept. Retalhuleu, Oct 1891, W. C. Shannon 593 (F); north of Nueva Linda, Dept. Retalhuleu, 18 Feb 1941, Standley 87758 (F); vicin. Retalhuleu, Dept. Retalhuleu, 17 Feb - 1 Mar 1941, Standley 88700 (F); below Colomba on road to Asintal, Dept. Quezaltenango, 20 Feb 1941, Standley 87893 (F); Colomba, Dept. Quezaltenango, 25 Sep 1934, A. Skutch 1305 (GH); San Francisco Miramar, Dept. Quezaltenango, 15 Mar 1921, Conduz Rojas 201 (US); Las Animas, Dept. Suchitepéquez, Sep 1891, Shannon 602 (US); Mazatenango, 28 Feb 1905, W. A. Kellerman 5144 (US); vicin. Mazatenango, Jun 1869, G. Bernoulli 542 (K, NY); vicin. Mazatenango, 18 Feb 1905, Maxon & Hay 3480 (US); Tequisate, Dept. Suchitepéquez, 19 Jun 1942, J. Steyermark 47863 (F); Pantín, below Tamahú, 5 Apr 1939, Standley 70838, 70824 (F); Finca Mocá, Alta Verapaz, 4 Dec 1919, Harry Johnson 84 (US, GH); Finca Mocá, 2 Apr 1931, J. Bequaert 39 (F, GH, NY, US); Guazacapán, Dept. Santa Rosa, 29 Nov - 3 Dec 1940, Standley 78598 (F); along Avellana road, S of Guazacapán, 6 Dec 1940, Standley 79430 (F); 4-5 km W of Escuintla, 15 Jul 1960, King 3372 (MICH, NY, TEX, US); San Luis, Dept. Escuintla, Mar 1890, J. Donnell Smith 2376 (F, GH, NY, US); Santa Barbara, Dept. Sololá, Aug 1891, Shannon 588 (US); Volcán de Tacaná, Dept. Amatitlán, 6 Apr 1921, Conduz Rojas 508 (M)).

HONDURAS: Río de la Orilla, SE of El Zamorano, 16 Oct 1949, Standley 24168 (F, US); Río Yeguaire drainage, Cerro

Majicoran, above Río de la Orilla, 16 Oct 1949, L. O. Williams 16942 (F, GH, US); San Lorenzo, Dept. Valle, 26 Aug 1945, J. V. Rodriguez 3247 (F, US); San Lorenzo, Dept. Valle, 10 Sep 1945, Rodriguez 3328 (F); Los Dragos, on Río Chamelecón, SW of Quimistán, Dept. Santa Barbara, 16-17 Apr 1947, Standley & Lindellie 7373, 7461 (F); San Pedro Sula, Dept. Santa Barbara, Dec 1888, C. Thieme 5315 (F, GH, NY, US); San Pedro Sula, Dept. Cortéz, 22 Jun 1952, A. Molina 5224 (F, US); San Pedro Sula, 10 Aug 1929, W. N. Bangham 303 (F, GH); Río Lindo, Peña Blanca, near Lake Yojoa, Dept. Cortéz, 8 Aug 1948, Williams & Molina 14561 (F, GH); 3 km from San Pedro Sula, 28 Nov 1950, Molina 3438 (F); vicin. Pespire, Dept. Choluteca, 18-25 Oct 1950, Standley 27067 (F); El Tigre Volcano, above Amapala, 16 Sep 1935, J. West 3547 (GH, MO).

EL SALVADOR: San Salvador, 1922, S. Calderón 808 (GH, NY, US); vicin. San Salvador, 30 Mar - 24 Apr 1922, Standley 23195 (GH, US); vicin. San Salvador, 20 Dec 1921 - 4 Jan 1922, Standley 19404 (GH, US), Standley 19622 (GH, NY, US); San Salvador, Jun 1906, L. V. Velasco 8904 (GH, US); San Marcos, Dept. San Salvador, 10 Jan 1946, Margery Carlson 5 (F, MO); near Apulo, Dept. San Salvador, 19 Jun 1949, Williams & Molina 16767 (GH, MO); road from San Martín to Laguna de Ilopango, 1 Apr 1922, Standley 22569 (GH, US); Vicin. of San Vicente, Dept. San Vicente, 7-14 Feb 1947, Standley & Padilla 3460, 3631 (F), 2-11 Mar 1922, Standley 21707 (GH, NY, US); vicin. Santa Emilia, Dept. Sonsonate, 22-25 Mar 1922, Standley 22089 (GH, NY, US); vicin. Izalco,

Dept. Sonsonate, 17 Feb 1907, H. Pittier 1921 (F, US); Montecristo, ca. 15 km NE of San Miguel, Dept. Morazán, 12 Dec 1941, J. M. Tucker 522 (F, US), Nov 1941, Tucker 429 (F); vicin. Ateos, Dept. de La Libertad, 17 Apr 1922, Standley 23385 (GH, US); La Unión, 21 Sep 1860, L. Wagner (GH); Finca San Nicolás, 1923, F. Choussy 64, 65 (US).

NICARAGUA: Managua, Oct 1932, Bro. A. Garnier A1352, A1362 (A, F), 1924, Bro. Artemio 33 (US), 2 Nov 1923, D. Chaves 49 (US); vicin. Managua, Aug 1932, Garnier 1150 (US); Sierra de Managua, Dept. Managua, ca. 1930-1940, A. Garnier (F); Masaya, Dept. Masaya, 27 Feb 1903, C. F. Baker 2207 (MO, US); Ameya, Dept. Chinandega, 19-21 Jun 1923, W. R. Maxon 7153 (GH, US); Realejo, Dept. Chinandega, 23 Jan 1903, Baker 2296 (GH, US); Island Ometepe, Lake Nicaragua, Jan 1893, C. L. Smith (GH, MICH); Mt. Mombacho, near Granada, 22 Dec 1940, Verne Grant 746 (A, F).

COSTA RICA: Prov. of Alajuela: Carrillos de Póas, 2 Nov 1931, A. M. Brenes 14581 (F, NY), 7 Dec 1931, Brenes 14625 (F, NY), 24 Sep 1933, Brenes 17205 (F, NY), 8 Oct 1933, Brenes 17241 (F, NY), 2 Dec 1931, Brenes 14598 (F); La Palma de San Ramón, 12 Nov 1925, Brenes 4629 (F, NY). Prov. of Cartago: Instituto Interamericano De Agrícolas, 20 Aug 1962, King 5339 (MICH, TEX, US). Broussailles á Nuestra Amo, llanos de Turúcares [Turrúcares], 15 Sep 1902, H. Pittier 16435 (US).

COLOMBIA: Dept. Magdalena: Río Frío (Santa Marta Mts.), Jul 1925, Fred Walker 1259 (US); Río Frío, 12 Nov 1926, G. Galt "D" (US); Río Frío, near railroad station, 12 Sep

1888-1901, H. H. Smith 593 (F, GH, K, MO, NY, US); Río Frío, between Ciénaga de Santa Marta and the foothills, 22-30 Jun, Pittier 1629 (F, US); Aracataca, 20 Jan 1940, Dugand & Barriga 2475 (US). Dept. Atlántico: between Sabanalarga and Campeche, 11 Jan 1941, Dugand & Jaramillo 2761 (US); Baranoa, Jul 1935, Bro. Elias 1327 (F, US); Usiacurí, Aug 1927, Bro. Elias 313 (US); Barranquilla, 27 Dec, Bro. Elias 457 (F); Barranquilla and vicin., 1927, Bro. Elias 338 (US); Nov 1928, Bro. Elias 604 (US); Palmar de Varela, 16 Jan 1930, Bro. Elias 764 (US); Santo Tomás, Jul 1932, Bro. Elias 1002 (F, GH, NY, US).

VENEZUELA: Cojedes, highway between San Carlos and Acarigua, 15 Nov 1940, C. E. Chardon 222 (US); between Valencia and La Entrada, Carabobo, 22 Dec 1938, Williams & Alston 377 (F, NY, US); Sabanas de Cujicito, Aug 1930, José Saer 566 (F).

PLATE X

SCLEROCARPUS SPATULATUS Rose, Feddema 1777 (MICH)

Fig. 1. Upper branch, x 0.6.

Fig. 2. Young capitulum, x 2 (Drawn from photograph).

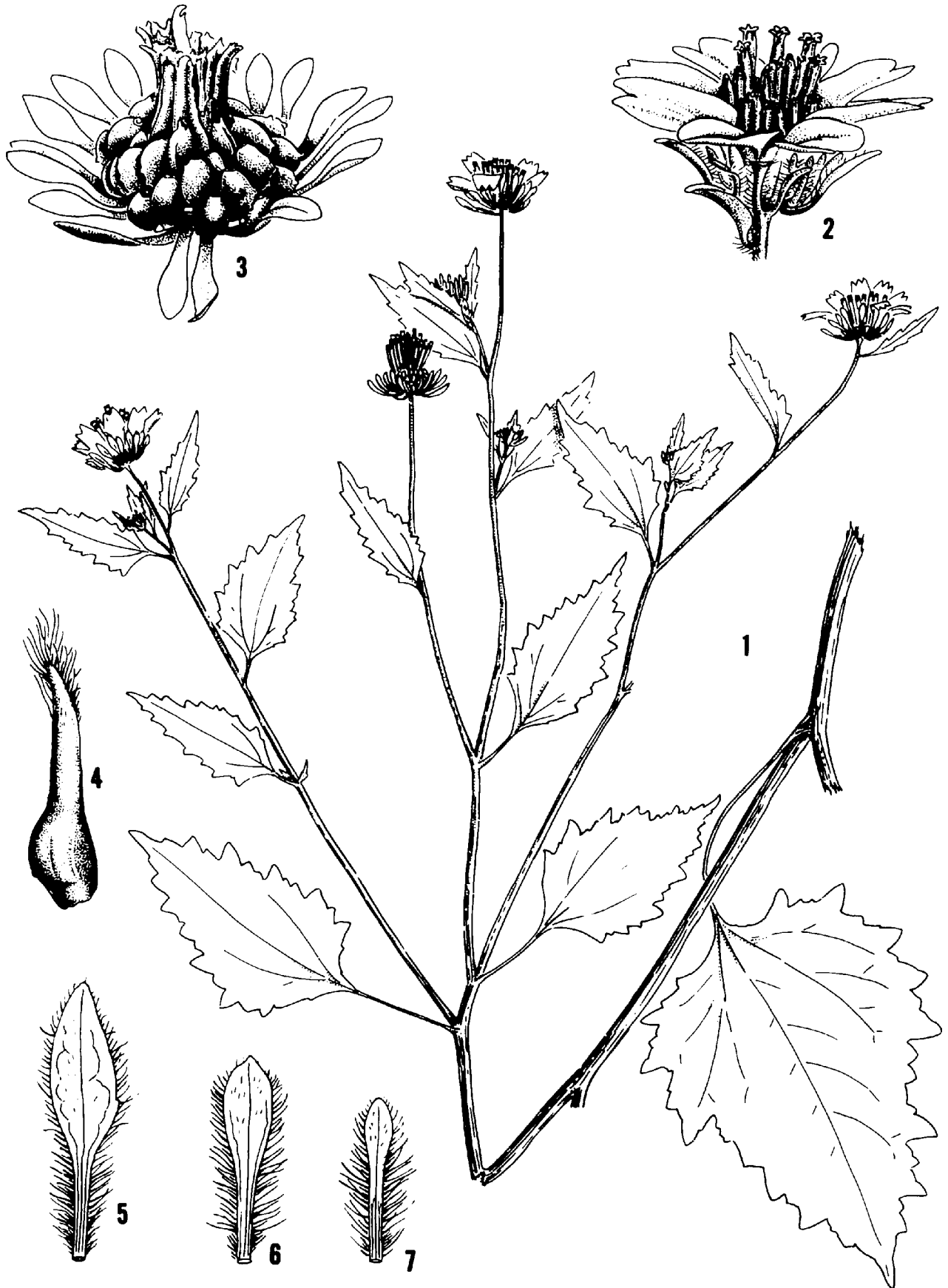
Fig. 3. Capitulum after fall of marginal disk corollas,
showing maturing receptacular bracts, x 3.

Fig. 4. Maturing receptacular bract from near the center
of the disk, x 6.

Fig. 5. Bract of the peduncle inserted close to the
involucre (adaxial surface), x 3.

Fig. 6. Outer involucre bract (adaxial surface), x 3.

Fig. 7. Inner involucre bract (adaxial surface), x 3.



3. *SCLEROCARPUS SPATULATUS* Rose, Contr. U.S. Nat. Herb.

1:103. 1891. Plate X.

Somewhat coarse, erect annual, (4-) 7-12 (-15) dm tall, the younger portions of the stem and branches strigose with white hairs to 0.8 mm long, with some crisped hairs mostly less than 0.2 mm long; pubescence of the very young branches and peduncles dense, with appressed or spreading hairs mostly less than 2 mm long; leaves, including the petioles, (4-) 7-12 (-20) cm long, the lower ones large, with petioles $1/2$ to nearly as long as the blade, the upper smaller, the petioles $1/4$ - $1/3$ (- $1/2$) as long as the blade; blades (2-) 5-9 (-12) cm long, (1-) 3-6 (-9) cm wide, narrowly to broadly ovate-trullate, the margin with (2-) 5-9 (-20) teeth on each side, the base cuneate, narrowly decurrent on the petiole, the apex acute, the surface scabrous adaxially with a few white, bulbous-based hairs mostly 0.3-0.5 mm long, and more numerous, crisped hairs less than 0.3 mm long, the abaxial surface strigose with white hairs mostly 0.3-0.9 mm long; heads few to several, 8-10 mm high, borne on the peduncle-like apex of the stem and branches; peduncles rarely naked, usually with one or more reduced leafy bracts; receptacle ovoid-conoid, 1-3.5 mm long, 2-5 mm diameter, the apex rounded, the pits with raised margins, these sometimes with a few hairs; involucre biseriate, or appearing triseriate, campanulate when young and 7-15 mm in diameter, becoming subrotate as achenes mature, frequently subtended by 1-2 (-7) lanceolate or oblanceolate bracts to 20 mm long

inserted on the peduncle or at the base of the involucre;
 involucral bracts 15-21, (5-) 8-13 (-17) mm long, (0.5-)
 1-2.5 (-3.2) mm wide, the inner linear-spatulate, one
 subtending each ray achene, the outer spatulate-oblongate,
 the surface sparsely scabrous-strigose adaxially, the hairs
 longest at base, strigose abaxially above the middle, with
 hairs to 1 mm long, the margin and base with coarse,
 spreading, whitish or hyaline hairs 1-2.5 (-3.5) mm long;
 ray flowers (6-) 7-8 (-9), (7-) 10-17 (-20) mm long,
 including the tube, spreading radially to 2 cm from the
 center of the disk; ligules orange yellow, becoming yellow
 in age, ovate-oblong, 11-17 mm long, 4-11 mm wide, nearly
 perpendicular to the tube, the apex with teeth 1-3 mm long,
 the abaxial surface sparsely strigulose with hairs to 0.7
 mm long; tube of the ray corolla short pubescent, 3-7 mm
 long; achenes of the ray flowers 2-4 mm long, green or
 whitish, fleshy throughout, arcuate, trigonous in cross
 section, often shriveled when dry; disk flowers 35-70,
 oriented in the head nearly parallel to the axis of the
 receptacle, the corolla 7-15 mm long, pale greenish yellow
 and 0.3-0.7 mm diameter at base, orange yellow and 0.7-1.8
 mm diameter at the lobes; lobes of the disk corolla 1.7-4.5
 mm long, the inner surface short yellow-papillate apically
 with a beard of blackish hairs below, these projecting
 beyond the margin of the lobes and visible as a black band
 around the corolla near the middle of the lobes; mature
 sclerocarps of the marginal 2-3 rows of disk flowers some-
 what laterally compressed, obliquely obovate in lateral

outline, 3.5-5 mm long, 2-3.5 mm measured radially, the apex of the sclerocarp forming a low irregular rim around the apex of the achene, the rim sometimes with an abaxial tooth on inner sclerocarps; surface of the sclerocarps green, purplish, mottled or black, with a few appressed hairs adaxially, a few curving ribs laterally, and conical tubercles on the abaxial ridge and laterally toward the apex; receptacular bracts of the inner 3-4 rows of disk flowers to 8 mm long, greenish, somewhat thickened at base, extending beyond the achene in a thin, greenish or yellowish trough-like blade, this sparsely strigose abaxially and with yellow, multi-celled cilia on the distal margin and tufted apically; achenes of the marginal 2-3 rows of sclerocarps slightly laterally compressed, obliquely obovate in lateral outline, 3-4.2 mm long, 1.7-3 mm measured radially, the base narrowed and strongly recurved upward, the apex crowned with a short cylinder, the pappus absent; chromosome number $n = 11$ (Feddema 1777, MICH).

Southern Sonora and southwestern Chihuahua, at elevations of approximately 100 to 1000 meters, flowering August to November.

Type: SONORA: Alamos, 16-30 Sep 1890, Edward Palmer 649 (Lectotype US! [specimen no. 47252] ; isotypes F! GH! NY! US!).

Of the four specimens in the type collection at The United States National Herbarium, specimen number 47252 is designated the lectotype. It is a good representative specimen with several heads in different stages of

development. Specimens numbered 47250, 47251 and 1400654 are designated isotypes.

This species is most closely related to Sclerocarpus divaricatus from which it differs conspicuously in having a biseriate involucre of long, spatulate bracts.

Specimens examined:

SONORA: 6 km W of Alamos, 21 Aug 1961, Feddema 1777 (MICH); 22 mi S of Moctezuma, 25 Sep 1934, I. L. Wiggins 7456 (GH, MICH, US); Ciudad Obregón, 29 Sep 1933, H. Gentry 296 (MICH); 11 mi NE of Colorado, 6 Sep 1941, Wiggins & Rollins 336 (A, MICH, MO, NY, US); San Bernardo, Río Mayo, 7 Sep 1939, Gentry 1677 (F, GH, MO, NY, US); Alamos, 29 Oct 1939, Gentry 4772 (NY); Canyon Sapopa, Río Mayo, 15 Oct 1934, Gentry 1041 (F, GH, MO).

CHIHUAHUA: Guasaremos, Río Mayo, 22 Aug 1936, Gentry 2407 (F, GH, MO).

PLATE XI

SCLEROCARPUS PAPPOSUS (Greenm.) Feddema

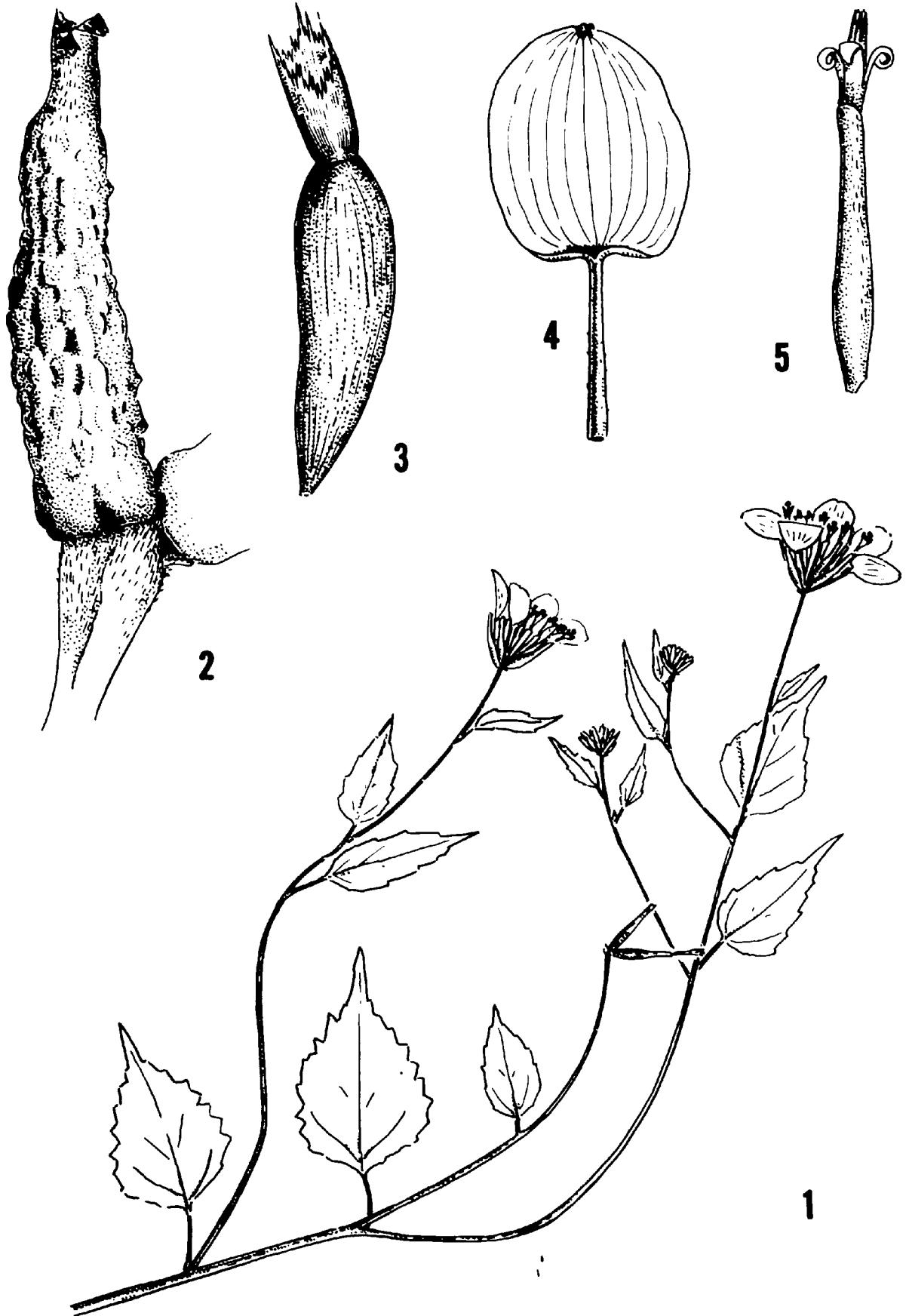
Fig. 1. Branch, x 0.8, R. Q. Abbott 402 (GH).

Fig. 2. Mature receptacular bract enclosing disk achene,
x 8, Y. Mexia 8707 (MO).

Fig. 3. Maturing disk achene with pappus, x 8, Orcutt 4208
(F).

Fig. 4. Ray corolla, flattened, x 4, Mexia 8707 (GH).

Fig. 5. Immature receptacular bract enclosing the disk
corolla, x 4, Mexia 8707 (GH).



4. *SCLEROCARPUS PAPPOSUS* (Greenm.) Feddema, comb. nov.

Plate XI.

Sclerocarpus uniserialis var. *papposus* Greenman, Field

Mus. Publ. Bot. 2:346. 1912.

Erect annual to 1 m tall, the branches long and slender, strigose with white hairs mostly less than 0.7 mm long; leaves (3-) 5-12 (-20) cm long, including the petioles; blades ovate-trullate or ovate-deltoid, (2-) 4-9 (-13) cm long, (1-) 2.5-7 (-12) cm wide, sparsely scabrous or scabrous-strigose adaxially, the abaxial surface mostly strigose, sometimes densely so with white hairs to 1.2 mm long; margin of the blade dentate with 7-15, somewhat irregular, mostly sharp teeth on each side, the apex attenuate, the base cuneate or obtuse; heads few to several, 10-20 mm high, on very slender, often curved peduncles to 6 cm long; receptacle conical, 1.5-3.5 mm long, 1.4-2.0 mm diameter, scarcely wider than the peduncle, the apex somewhat pointed, the surface green, hispidulous between the pits with stiff white hairs; involucre very inconspicuous, sometimes scarcely detectable, the bracts 3-7, (1-) 1.5-2.0 (-3.5) mm long, appressed to the ray flowers or reflexed in age, linear or narrowly elliptic-oblongate when young, becoming rolled, acicular and hairlike in age, the surface gray, strigose, with white hairs mostly less than 0.5 mm long; ray flowers 3-7, 14-20 mm long, including the tube, spreading to 1.5 cm from the center of the disk; ligule yellow orange, mostly broadly ovate, (4-) 6-12 mm long, (5-) 7-11 mm wide, the apex with 2-3 minute teeth,

the abaxial surface strigulose with hairs mostly 0.3-0.9 mm long; tube of the ray corolla green, sometimes arcuate, mostly less than 0.7 mm diameter, 6-12 mm long, longer or nearly as long as the ligule; ray achenes green, 0.7-1.5 mm long, fleshy throughout, glabrous or strigose; disk flowers (4-) 6-12 (-15), often somewhat arcuate, oriented in the head to form an inverted cone including an angle of approximately 50-80 degrees; disk corollas 8-14 mm long, 0.5-0.8 mm diameter at base, 1-2 mm diameter at the lobes, the outer surface green or yellow under the enclosing bract with hairs less than 0.1 mm long, the upper portion of the tube glabrous, usually with a brownish or reddish area' often extending on to the lobes; lobes of the disk corolla brownish or reddish outside at base or to the middle, the upper portion yellow with a few stiff appressed hairs to 0.3 mm long, the apex strongly reflexed or recurved, the inner surface yellow with short papillae at the apex, these to 0.4 mm long near the middle of the lobe and along the margin; anthers dark colored, exserted well beyond the mouth of the corolla at anthesis; immature sclerocarps 8-11 mm long, thin, green, arcuate, tubular, loosely enclosing the achene and corolla, sometimes reaching to the base of the corolla lobes, the outer surface with white appressed hairs mostly less than 0.5 mm long; maturing sclerocarps with the basal one-half swelling to accomodate the enlarging achene, the upper one-half forming a tapered tubular beak; mature sclerocarps to 13 mm long, cylindroid or long-conoid, slightly arcuate, 2-3 mm diameter at base,

gradually tapering toward the apex, there reduced to form a short narrow beak 2-3 mm long, sometimes constricted about the apex of the achene and enlarged again about the pappus; surface of the sclerocarp brown, greenish or purple-mottled, sparsely strigose, with prominent longitudinal ribs the length of the body, these sometimes tubercled; achenes of the disk flowers 7-11 mm long, including the pappus, fusiform, slightly arcuate, sometimes laterally compressed, slightly curved at the point of attachment, the pappus a conspicuous green or yellowish tube or crown of fused bristles of varying length, mostly 1.7-4 mm long, the margin very irregular.

Guerrero, at elevations of approximately 500 to 2000 meters, flowering August to October.

Type: GUERRERO: Río Balsas, 25 Aug 1910, C. R. Orcutt 4208 (Holotype F!; isotype MO!).

This species is most closely related to S. uniserialis of which Greenman regarded it as a variety. It differs from that species in its very long pappus, its longer, nearly straight sclerocarps, the extremely reduced involucre and the small hairy receptacle. It is apparently a rare species and poorly known, having been observed only from the type collection and two others.

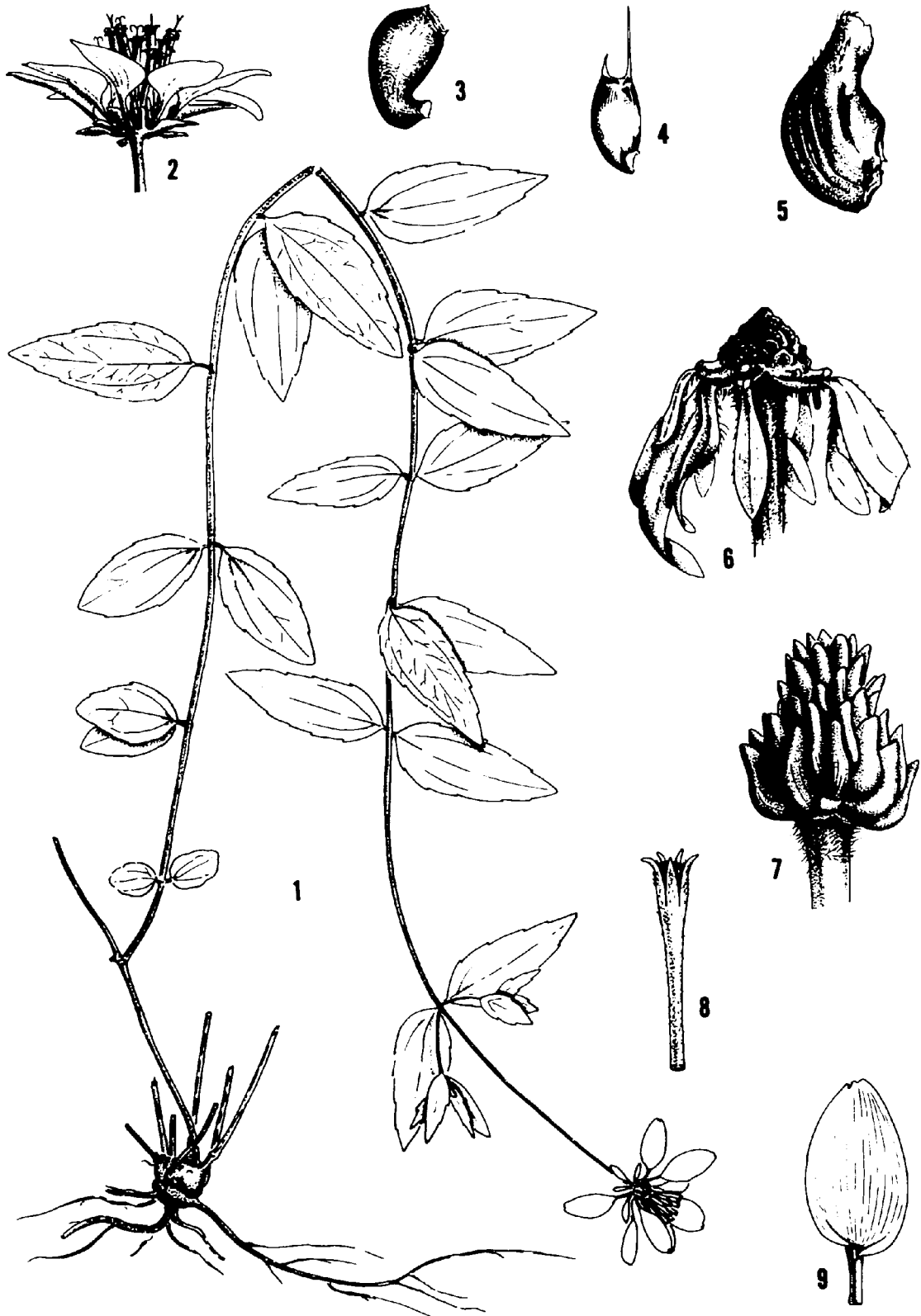
Specimens examined:

GUERRERO: North of Río Balsas, Dist. Adama, Temisco, top of Barranca Limo, 30 Oct 1937, Ynez Mexia 8707 (F, GH, MO, NY, US); Taxco Viejo, 18 Sep 1937, R. Q. Abbott 402 (GH).

PLATE XII

SCLEROCARPUS SESSILIFOLIUS Greenman

- Fig. 1. Habit sketch, x 0.5, Feddema 1426 (MICH).
- Fig. 2. Young capitulum, x 0.9, Feddema 1758 (MICH)
(drawn from photograph).
- Fig. 3. Achene of marginal disk flower, x 5, Mexia 837
(MICH).
- Fig. 4. Achene of central disk flower, x 5, Mexia 837
(MICH).
- Fig. 5. Receptacular bract enclosing marginal disk achene,
x 5, Mexia 837 (MICH).
- Fig. 6. Receptacle showing ray achenes and involucral
bracts after dehiscence of receptacular bracts and
achenes, x 2.5, Feddema 1758 (MICH).
- Fig. 7. Young receptacle showing bracts, x 2.5 (disk
corollas, ray flowers, and involucral bracts removed),
Feddema 1758 (MICH).
- Fig. 8. Disk corolla, x 1.5, Feddema 1758 (MICH).
- Fig. 9. Ray corolla, x 1.5, Feddema 1758 (MICH).



5. *SCLEROCARPUS SESSILIFOLIUS* Greenman, Proc. Am. Acad.
40:38. 1904. Plate XII.

Weak-stemmed perennial, (2-) 5-10 (-12) dm long; stem erect or decumbent in youth with 1-3 short upper branches, procumbent or reclining at maturity with well-developed basal branches; branches mostly opposite, usually alternate near apex, the lower long, procumbent or ascending, often longer than the stem; base of the stem forming a woody tuber near the surface of the soil, this becoming hard, to 2 cm diameter, subglobose or irregular, often exposed on the surface of the soil; mature plant dying back from apex, sometimes consisting only of procumbent secondary or tertiary basal branches, eventually dying to base with new shoots arising from the tuber; basal portions of stem and branches woody in age, the surface gray, glabrate, or younger portions of the stem yellowish or purplish, hispidulous with whitish or yellowish multi-celled bulbous-based hairs 0.5-1.5 (-2.5) mm long, the peduncles with somewhat spreading hairs, especially below the involucre; leaves (2-) 3-5 (-8) cm long, longest near the middle of the stem and branches, those on or near the peduncles much reduced; petioles (1-) 2-4 (-6) mm long, mostly $1/6$ - $1/10$ as long as the blade; blades (1-) 3-6 (-7.5) cm long, (0.7-) 1-2 (-3.5) cm wide, mostly lanceolate, occasionally elliptic, those of the uppermost leaves narrowed, those of the lowermost sometimes ovate; margin of the blade coarsely or shallowly serrate with (2-) 3-6 (-9) mostly regular, glandular-tipped teeth, rarely subentire, the apex of the

blade acute, rarely obtuse, the base cuneate or rounded, the adaxial surface with curving yellowish hairs mostly 0.6-1.2 mm long, the abaxial surface more densely scabrous-strigose with curving, whitish, subappressed hairs; heads few, 15-23 mm high, on straight or ascending, mostly naked peduncles to 25 cm long; receptacle low-conoid, 3-5.5 mm high, 3-6 mm diameter, the apex blunt, the surface with rhombic-ovate pits with raised margins, these slightly pubescent when young, glabrate in age; involucre essentially uniseriate, subcampanulate, 10-20 mm diameter when young, enlarging and rotate at maturity, reflexed in age after shedding of sclerocarps; involucral bracts 7-18, one subtending each ray achene, (4-) 7-11 (-20) mm long, (1-) 2-4 (-6) mm wide, linear-lanceolate or oblanceolate-spatulate, the apex acute, coarsely scabrous adaxially, strigose-scabrous abaxially with mostly subappressed hairs 1-1.8 mm long; ray flowers (7-) 8-10 (-16), 11-35 mm long, including the tube, spreading to a radius of 2.8 cm from the center of the disk; ligules bright yellow, rarely yellow orange, (6-) 8-16 (-26) mm long, 4-15 mm wide, mostly oblong-ovate, rarely elliptic, obovate or subcircular, the apex with 2-4 shallow, rounded or long sharp teeth to 5 mm long, sparsely short-strigulose adaxially with hairs mostly less than 0.3 mm long, often with brownish veins; tube of the ray corolla 3-9 mm long, 0.4-1.3 mm diameter, with hairs less than 0.3 mm long; ray achenes (0.3-) 1-1.5 (-2.7) mm long, greenish or white when living, shriveled when dry; disk flowers 28-70, 8-15 mm long, oriented in the head nearly

parallel to the axis of the receptacle or somewhat spreading at apex; disk corollas greenish yellow and 0.5-1.5 mm diameter at base, orange yellow and 1.7-2.1 diameter at the lobes, with yellowish hairs to 0.4 mm long, the lobes 3-4 mm long, short yellow-papillate within at apex, with a beard of dark or blackish hairs below, these projecting beyond the margin of the lobe and visible as a black band about the corolla near the middle of the lobes; mature sclerocarps of the marginal 1-2 rows of disk flowers short-beaked, 3-6 mm long, 1.5-3.5 mm measured radially, the body slightly laterally compressed, obliquely obovate-oblong in lateral outline, brown or yellowish and glabrate at base, darker brown and griseous above, prominently ribbed abaxially and laterally; the beak 1-2 mm long, thin-walled, tubular, bent adaxially, extending beyond and concealing the achene, greenish or brown, griseous pubescent with short spreading or crisped hairs; receptacular bracts of the central disk graduate, to 8 mm long; mature achenes of the marginal 1-2 rows of sclerocarps somewhat laterally compressed, obliquely obovate in lateral outline, 2.5-4.5 mm long, 1.2-2.5 mm measured radially, brownish or black, the base narrowed and slightly curved upward, the pappus a yellowish crown of fused bristles or a fimbriate rim, this 0.1-0.2 mm long laterally, lengthening abaxially and adaxially to form angular scales or teeth to 0.5 mm long; achenes of the central disk obliquely fusiform-cylindroid, the pappus with adaxial scales becoming awn-like to 4 mm long; chromosome number, $n = 14$ (Feddema 1758, MICH).

Nayarit, Sinaloa, and western Durango at elevations of 600 to 2400 meters, flowering July to November.

Type: SINALOA: foothills of the Sierra Madre, between Rosario and Colomas, 13 Jul 1897, J. N. Rose 1629 (Lectotype GH!; iso-lectotype US!).

Greenman, in the original description of this species cited Rose 1629 and Rose 3224 from both the Gray Herbarium and the U.S. National Herbarium. The sheet which Greenman presumably saw at the Gray Herbarium contains specimens of both of these collections. Rose 3244, however, is only a vegetative fragment, whereas Rose 1629 is a readily identifiable branch with a complete head in flower. For this reason, J. N. Rose 1629 at the Gray Herbarium is designated as the lectotype.

Specimens examined:

NAYARIT: above the lake, NE of Santa María del Oro, 18-20 Aug 1959, Feddema 617A (MICH); Rancho San Isidro, ca. 10 mi E of Jesús María, 22 Sep 1960, Feddema 1462 (MICH); near Santa María del Oro, 19 Aug 1961, Feddema 1758 (MICH); 2 mi NE of Santa María del Oro, 15-16 Sep 1960, R. McVaugh 19082 (MICH); SW of Tepic, 18-19 Aug 1935, F. W. Pennell 19790 (US); 10 mi SE of Tepic, 30 Aug 1957, McVaugh 16587 (MICH); trail from San Marcos to Yxtlán [Istlán], 29 Sep 1926, Y. Mexia 837 (F, GH, MICH, MO, NY, US); 8 mi SE of Tepic, 10 Aug 1960, R. M. King 3673 (MICH, NY, TEX, US); Tecolote, 3 Oct 1923, Collins & Kempton 49 (US).

SINALOA: highway from Villa Unión to Durango, ca. 40 km W of the Sinaloa-Durango boundary, 22 Aug 1961, Feddema 1805

(MICH); Ocurahui, Sierra Surotato, 1-10 Sep 1941, H. S. Gentry 6410 (GH, MICH, MO, NY); Las Mesas, Sierra Surotato, 25 Aug 1941, Gentry 6137 (GH, MICH, MO, NY); San Juan, 1921, J. G. Ortega 4015 (US); Cerro de la Prieta Choix, 1921, Ortega 3048 (US); near Colomas, 20 Jul 1897, J. N. Rose 3224 (GH, US); Cuantantal, Concordia, Sep 1919, M. P. Dehesa 1538 (US); Camino para la Tigra, San Ignacio, 12 Aug 1918, A. E. Salazar 447 (US); Batel, Concordia, Oct 1919, J. A. Partida 2025 (US).

DURANGO: La Bajada, Tamazula, Nov 1921, Ortega 4431 (US).

PLATE XIII

SCLEROCARPUS AFRICANUS Jacq. ex Murray

Fig. 1. Ray corolla, x 5, (drawn from plants grown at the Botanical Gardens of the University of Michigan from seeds of H. Wild 5760).

Fig. 2. Ray corolla, x 5 (drawn from pressed specimen of above).

Fig. 3. Capitulum with ray flowers removed, x 2.5 (drawn from living plant of fig. 1.).

Fig. 4. Disk corolla, x 5 (drawn from living plant of fig. 1.).

Fig. 5. Marginal disk achene, x 5, M. A. Siddigi 1459 (MICH).

Fig. 6. Marginal receptacular bract enclosing the achene, lateral view, x 5, Siddigi 1459 (MICH).

Fig. 7. Receptacle after fall of disk achenes, x 2.5 (outer involucre bracts and one ray achene removed), drawn from living plant of fig. 1.

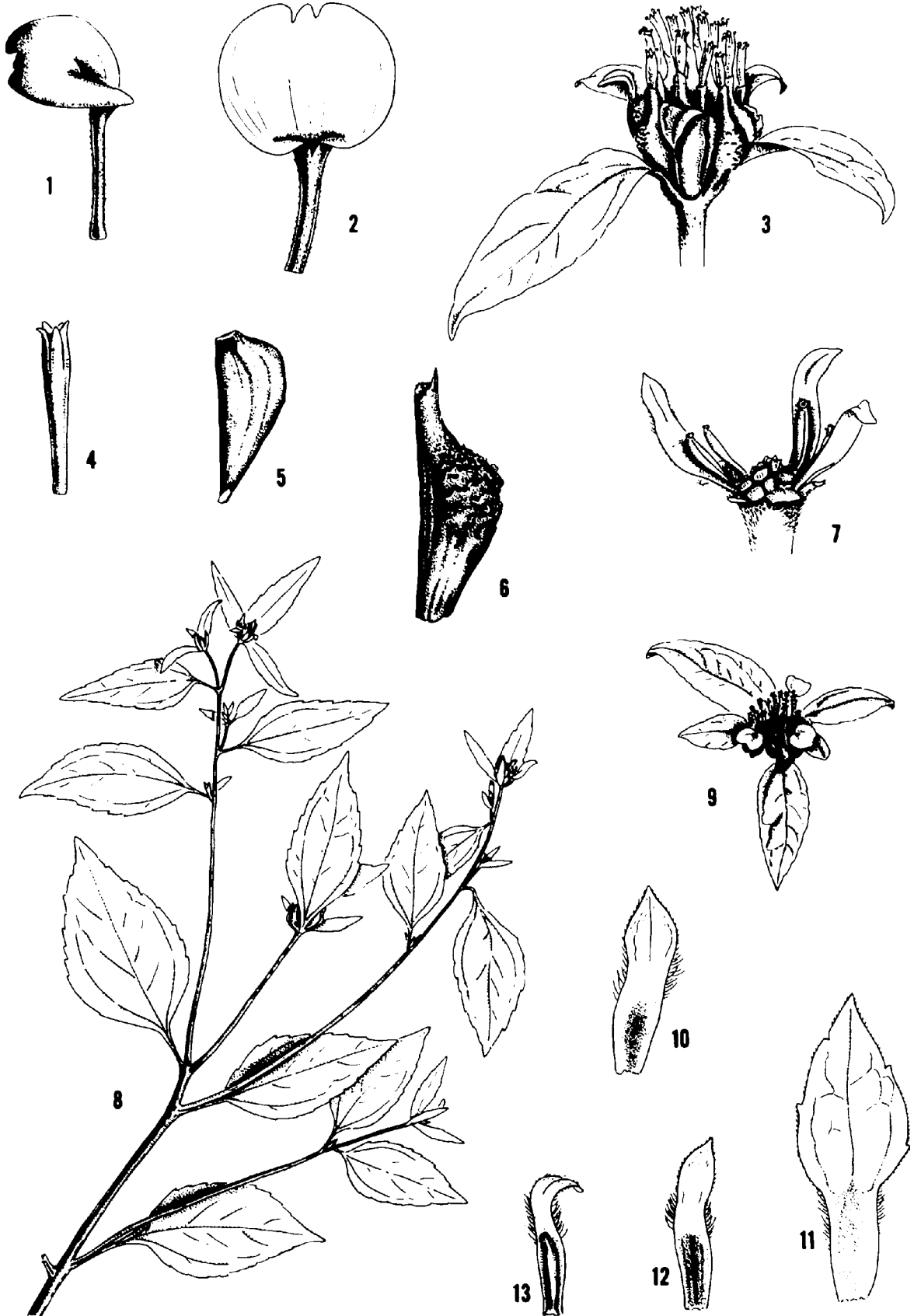
Fig. 8. Apical portion of plant, x 0.5, R. R. Stewart 14951 (NY).

Fig. 9. Mature living capitulum, x 1 (drawn from living plant of fig. 1.).

Figs. 10, 11, 12. Involucre bracts, pressed, x 2.5 (drawn from plant of fig. 1.).

Fig. 13. Smallest involucre bract with ray achene, x 2.5, (drawn from living plant of fig. 1.).

Plate XIII



6. *SCLEROCARPUS AFRICANUS* Jacquin ex Murray, Syst. Veg.
ed. 14. 783. 1784. Plate XIII.

Melampodium baranguillae Spreng. Syst. Veg. 3:619. 1826.

Type: "ad fl. Magdalenae", Bertero (Holotype P;
photograph of holotype, GH! US!).

Sclerocarpus columbianus Rusby & Blake, in Blake, Contr.

U.S. Nat. Herb. 22:609. 1924. Type: COLOMBIA: Ciénaga,
vicin. Santa Marta, 6-12 Sep 1898-1899, H. H. Smith 518
(Holotype NY!; isotypes GH! MICH! MO! US!).

Sclerocarpus baranguillae (Spreng.) Blake, Contr. U.S.

Nat. Herb. 26:242. 1930.

Erect annual, (1-) 3-8 (-13) dm tall; stem usually
well-branched (slender and unbranched in impoverished
specimens), branching rarely opposite nearly to apex;
older portions of the stem glabrate or sparsely strigose-
hispidulous, younger portions of branches and peduncles
with short crisped or appressed hairs, some longer
appressed hairs to 0.7 mm long, and some yellowish appressed,
spreading or erect hairs to 1.5 mm long, pubescence densest
just below the involucre; leaves (3-) 4-10 (-15) cm long,
including the petiole; petioles approximately (1/5-)
1/4-1/3 as long as the blade, the lower portion sometimes
narrowly margined; blades lanceolate or ovate, (2-) 3-8
(-12) cm long, (0.5-) 1.5-3.0 (-6) cm wide, the apex acute-
acuminate, the extreme tip sometimes rounded or blunt, the
base cuneate-attenuate, decurrent on the petiole, the
margin serrate, with (3-) 5-8 (-20) shallow teeth on each
side, the surface scabrous-strigose adaxially with mostly

subappressed hairs 0.6-1.3 mm long, strigose abaxially with whitish or yellowish hairs to 1.3 mm long; heads few to several, on mostly naked peduncles to 6 cm long, these often enlarged below the involucre; receptacle low-conoid, 1-3 mm high, 3-5 mm diameter, the apex blunt, the pits shallow with dark margins sometimes raised abaxially to the pits; involucre subcampanulate when young, spreading or reflexed at maturity, essentially uniseriate or appearing biseriate; involucre bracts 4-9, variable, graduate in size, form and disposition on the receptacle; innermost bracts smallest, the basal $2/3$ - $3/4$ whitish, linear, petiole-like, as long as the sclerocarps and appressed to them, the apex green, blade-like, spreading; outer bracts short-petiolate, spreading, often indistinguishable from the upper leaves; ray flowers 3-5, 3.8-10 mm long, including the tube, this about as long as the ligule; ligules yellow or orange, (2-) 3-5.5 mm long, (1.7-) 3-5.5 mm wide, broadly ovate or subcircular, bent nearly perpendicular to the tube, scarcely extending beyond the disk, sparsely short-strigose abaxially, the apex recurved; ray achenes 3-7 mm long, 0.5-1.5 mm wide, green, fusiform, arcuate, somewhat trigonous, hollow with fleshy walls when living, brownish or semitransparent, thin, flattened against the subtending bract when dry, the apex remaining broad; disk flowers 5-30, the corollas 3.5-8 mm long, 5 (-7) nerved, rarely 10-nerved or incompletely so, green, glabrous, 0.2-0.7 mm diameter at base, greenish or yellow, 0.7-1.8 mm diameter above with thin-walled hairs, these twisted or

flattened when dry; lobes of the disk corolla 0.8-2.2 mm long, yellow, the pubescence similar to the tube, or with short bristles at apex, the inner surface short-papillate apically and longer yellowish multi-celled hairs below and marginally, the hairs flattened and twisted when dry; mature marginal sclerocarps (3.9-) 6-10 (-13) mm long, 2-4 mm measured radially, widest above the middle in lateral outline, with a beak (1-) 2-4 mm long, scarcely bent from the body, the body narrowed to base, sharply narrowed to beak, green, brownish, rarely purple black, usually with a few whitish hairs abaxially above; surface of the sclerocarp longitudinally ribbed at base (the entire body striate if achenes do not develop), the upper portion laterally and abaxially with irregular undulating transverse grooves or interconnected pits, the lower margin of the groove an irregularly toothed ridge partly overlying the groove; mature achenes of the marginal disk flowers 3.5-8 (-10) mm long, 1.5-3.2 mm measured radially, somewhat laterally compressed, obliquely obovate-turbinate, narrowed gradually to base; pappus usually absent at maturity, sometimes with a few hairs or fused bristles abaxially when young; chromosome number, $n = 18$ (counted from offspring of H. Wild 5760).

Saint Thomas (U.S. Virgin Islands), northern Colombia near Barranquilla, northeastern Venezuela, Tropical West Africa from Ghana to Angola, East Africa from Ethiopia to Tanganyika and Rhodesia, West Pakistan and Northern India, at elevations from sea level to 1700 meters, flowering from August to April.

Type figure: Jacquin, Icones Plantarum Rariorum, t. 176. 1781.

The plant from which Jacquin's plate was drawn was presumably grown in a botanical garden in Vienna (Stearn, 1961), although no specimen was cited.

This species is most closely related to Sclerocarpus phyllocephalus from which it is distinguished by its greater height, coarser appearance, the form and size of the receptacular bracts, and the presence of a pappus in the juvenile stage.

Specimens examined:

WEST INDIES: SAINT THOMAS: Dec 1880, H. Eggers 282 (GH); 1887, Eggers (F); Jan 1887, Eggers (US); Aug 1887, Eggers (US); May 1888, Eggers 69 (GH, US); Eggers 374 (NY); beach near Charlotte Amalia [Charlotte Amalie], 8-9 Feb 1913, N. L. Britton 483 (MO, NY).

COLOMBIA: DEPT. ATLANTICO: Barranquilla and vicinity, Oct 1928, Bro. Elias 568 (US); near Barranquilla, 26 Sep 1954, A. Dugand 4827 (US); near Barranquilla, 27 Sep 1960, Dugand 5324 (US).

VENEZUELA: STATE OF MONAGAS: Buena Vista between Maturín and the sea, Sep 1963, F. Tamayo 4647 (US).

GHANA: Yendi, 30 Dec 1954, J. K. Morton A1411 (K).

NIGERIA: Jos Plateau, H. V. Lely P839 (K); Obu, 1911, N. W. Thomas 440 (K); "West Africa by the Niger", O. Hagerup 736 (K); "Baikie's Niger Expedition, 1957-1859", C. Barter 1294 (GH, NY).

DAHOMEY: M. G. Le Testu 41 (K).

ANGOLA: Distr. Golungo Alto, F. Welwitsch 3941 (K);
Distr. Mossamedes, 1859, Welwitsch 3939 (K).

ETHIOPIA: Ins Dalae? 1825, G. Ehrenberg 376 (GH).
River Tacaze and nearby mountains, M. W. Schimper 1648
(GH, K); "envoie de M. W. Schimper 185 No. 408" (K).

SUDAN: "in valibus provinciae Modat", 1839-1842,
Schimper 1035 (NY); Blue Nile Prov., Jekel Tozi, Sep 1953,
J. D. Lea 220 (K); Kordofan Prov., Arasch-Cool, "Mt.
Cordofan", 1839-1842, Kotsch 120 (GH, MO, NY).

ERITREA: Mont Ghedem, near Massawa, 6 Feb 1892, G.
Schweinfurth 103 (K).

SOMALIA: "Benadir-Giumbo", 1909, A. Fiori 57 (A).

KENYA: Athi River, 22 mi S of Mtito Andei, Bally 4714 (K).

TANGANYIKA: Rukwa, Rift Valley, Tilepa[?] 20 Mar 1947,
D. P. Pielou 169 (K).

NORTHERN RHODESIA: Machili, 2 Feb 1961, D. B. Fanshawe
F6249 (K).

SOUTHERN RHODESIA: Wankie, 19 Jun 1934, Eyles 8019 (K);
Distr. Darwin, upper reaches of the Nyatandi River, 27 Jan
1960, J. R. Phipps 2439 (MO); Distr. Urungwe, Zambesi Valley,
Rifa River, 24 Feb 1953, H. Wild 4083 (MO).

WEST PAKISTAN: Rawalpindi Distr., Nurpur, 20 Oct 1962,
M. A. Siddigi 1459 (MICH).

INDIA: NORTHWEST HIMALAYA: Tehri Garhwal, Jumabridge,
Sep 1898, J. S. Gamble 27202 (K); "Himalaya", 1844, M. P.
Edgeworth (K); Punjab, Kangra Distr., Dhamtal[?], 15 Oct
1934, R. N. Parker 3316 (GH); west of Jabberkhet (near
Mussooree) Aug 1935, R. R. Stewart 14951 (A, NY);

Mussoorie [Mussooree], 29 Aug 1935, Stewart 15006 (A, NY);
Aglar River, below Mussooree [Mussoorie], 26 Aug 1929,
Stewart 11374 (NY); north slope, Mussoorie, 31 Aug 1944,
Stewart 21246a (NY).

PLATE XIV

SCLEROCARPUS PHYLLOCEPHALUS Blake, S. S. White 5109 (MICH)

Fig. 1. Receptacle and involucre, x 2.5.

Fig. 2. Ray achene, x 5.

Fig. 3. Disk corolla, x 5.

Fig. 4. Mature marginal receptacular bract enclosing the
achene, lateral view, x 5.

Fig. 5. Mature marginal receptacular bract in longitudinal
section, showing the enclosed achene, x 5.

Fig. 6. Habit sketch, x 0.5.

Fig. 7. Ray corolla, x 5.



7. *SCLEROCARPUS PHYLLOCEPHALUS* Blake, Contr. U.S. Nat.

Herb. 24:27. 1922. Plate XIV.

Erect herbaceous annual, 1-4 (-10) dm tall, usually well-branched, occasionally branched only above (sometimes a single slender unbranched stem in impoverished specimens), usually the lower branches long, decumbent, procumbent or ascending, the stem glabrate or with worn hair bases basally, young branches strigose-hispidulous with yellowish hairs, youngest branches and peduncles often densely strigose-pilose; leaves 2-5 (-11) cm long, including the petioles, the petioles mostly $1/6$ - $1/3$ ($-1/2$) as long as the blade, sometimes narrowly margined; blades (1-) 2-4 (-8) cm long, 1-2 (-5) cm wide, ovate-lanceolate, rarely elliptic, the margin mostly serrate with (2-) 4-8 (-12) teeth on each side, rarely subentire, the apex acute-acuminate, rarely rounded, the base cuneate-attenuate, often decurrent on the petiole, scabrous-strigose adaxially with hairs mostly less than 1 mm long, strigose abaxially with hairs to 1.3 mm long, young blades often densely strigose-pilose with yellow hairs; heads one to several, 6-15 mm high, on mostly naked peduncles 1-6 (-11) cm long, these often enlarged at the involucre; receptacle low-conoid, (0.5-) 3-4 mm diameter, mostly wider than high, the apex blunt, the pits shallow, subcircular, dark margined; involucre subcampanulate in bud, spreading in age, essentially uniseriate or appearing biseriate; bracts of the involucre 6-12 (-15) graduate in size, form and disposition on the receptacle, the innermost smallest, mostly 5-12 mm long, 1-3 mm broad, the lower

portion whitish, linear, appressed to the developing sclerocarps, the apex green, expanded and spreading, intermediate bracts with the expanded upper portion larger and more spreading, the largest bracts inserted at the base of the involucre, lanceolate, spreading, scarcely distinguishable from the upper leaves, pubescence of all but the largest bracts conspicuous, of long whitish spreading hairs to 2.5 mm long and tufts of longer hairs adaxially near the base of the expanded portion; ray flowers (3-) 4-6 (-8), (3.5-) 6-9 (-10.5) mm long, including the tube, the tube short-pubescent, 1/2 to nearly as long as the tube, the ligule (2-) 3-5 (-7) mm long, (2.5-) 4-7.5 mm wide, yellow or orange, broadly ovate or subcircular, bent nearly perpendicular to the tube, the apex with 2-3 irregular teeth to 1 mm long; achenes of the ray flowers 2-4 mm long, fusiform, arcuate, greenish, hollow, sub-trigonus when living, minutely pubescent, thin, transparent and flattened when dry, the apex remaining broad; disk flowers (3-) 7-20 (-30), the corolla 5-nerved, yellow or orange, 5-10.5 mm long, 0.2-0.5 mm diameter at base, 1-2 mm diameter at the lobes, mostly short-pubescent, the lobes 1.2-2.6 mm long, the apex slightly spreading, sometimes purplish, the inner surface short-papillate apically and with thin-walled hairs to 0.4 mm long above the middle of the lobe and papillae of intermediate length below; anther sacs mostly 1.2-2.5 mm long; mature marginal sclerocarps (4.5-) 6-8 mm long, 2-3.5 mm measured radially, widest at or below the middle in lateral outline, with a beak 1.6-4 mm

long, often as long as the body and sharply bent from it, the body 3-4.7 mm long, narrowed to base, strongly obliquely obovate-turbinate in lateral outline, green, brownish, rarely purplish mottled, strigose, hispidulous or with additional short crisped hairs; surface of the sclerocarp often with longitudinal ribs basally, the upper portion usually strongly sculptured, especially abaxially, with irregular pits and a few flattened, angular or contorted tubercles below the pits; mature achenes of the marginal disk flowers 3.5-4.2 (-4.6) mm long, 1.5-2.5 mm measured radially, obliquely obovate-turbinate, narrowed at base, the surface black, shining or dull grayish; pappus none, rarely only suggested by low irregularities or a few hairs at the point of dehiscence of the corolla tube; receptacular bracts of the central disk to 11.5 mm long, the beak as long or longer than the body, the surface often merely striate, especially if the enclosed achenes fail to develop.

Southeastern Guatemala, southern Honduras, southeastern Nicaragua, at elevations of 200 to 1100 meters, flowering throughout most of the year although probably scarce in December and January in most localities.

Type: GUATEMALA: Dept. Izabal, Cristina, 23 May 1919, S. F. Blake 7648 (Holotype US!).

The holotype of this species is a particularly luxuriant specimen. Specimens having such large leaves and involucre bracts and such fullness of growth are apparently rare. This species is most closely related to

S. africanus. At the present time the two are nowhere sympatric. These two species can generally be distinguished by the larger size of the sclerocarps and achenes of S. africanus but some specimens are poorly differentiated on the basis of this character. Similarly, S. phyllocephalus is generally a small plant of 3-4 dm whereas S. africanus usually approaches one meter in height, but this is not universally true. The sclerocarps of each species do, however, have characteristic form and sculpturing. Sclerocarps of S. africanus have a long body and a short beak which is scarcely bent from it. The tubercles are numerous and resemble low ridges. In the sclerocarps of S. phyllocephalus, the beak is nearly as long as the body and bent sharply from it and the tubercles are few and long.

Specimens examined:

NICARAGUA: Lago Julia, Tamagasta Peninsula, W of Managua, 25 Jun 1923, W. R. Maxon 7307 (US).

HONDURAS: Dept. Comayagua: Río Selguapa, 22 Mar 1945, J. V. Rodríguez 2556 (F, US); Dept. Morazán: drainage of Río Yeguaré, Zamorano, 27 Jul 1948, S. F. Glassman 2057 (F, TEX); Zamorano, Aug 1944, Rodríguez 90 (F); vicin. El Zamorano, 1 Feb 1944, P. C. Standley 16048 (F), 14 Apr 1949, Standley 18999 (F, NY), 3-17 Aug 1947, Standley 11698 (F), 17 Feb - 8 Mar 1947, Standley 3897 (F), 16 Jul 1949, Standley 21326 (F), 26 Jul 1949, Standley 21744 (F, US); El Jicarito, above El Zamorano, near Río Caparrosa, 19 Jul 1949, Standley 21408 (F), 20 Jul 1949, Standley 21507 (F);

old road between Tegucigalpa and Suyapa, 6 Nov 1948, A. Molina R. 1452 (F), 6 Nov 1948, Standley 14172 (F); La Leona, Tegucigalpa, 6 Sep 1951, Standley 28677 (F); road between El Jicarito and El Pedregal, 13 Nov, Standley 14493 (F).

GUATEMALA: Dept. Zacapa: Zacapa, 24 Jan 1905, C. C. Deam 192 (GH, MICH); vicin. Zacapa, 7-16 Oct 1940, Standley 73592, 74149 (F); desert near Estanzuela, 5 Oct 1939, J. A. Steyermark 29075 (F, MICH); near electric plant of Río Hondo, base of Sierra de las Minas, 11 Oct 1940, Standley 73992 (F); Río Teculután, above Teculután, 7 Jan 1942, Steyermark 42163 (F, GH); road between Agua Blanca and Cumbre de Chiquimula, 15 Oct 1940, Standley 74429 (F). Dept. Izabal: Cristina, 23 May 1919, S. F. Blake 7642 (GH, US); Montaña del Mico, between Milla 49.5 and ridge 6 miles from Izabal, 1 Apr 1940, Steyermark 38594 (F). Dept. Chiquimula: llanos around Ipala, 23 Oct 1939, Steyermark 30332 (F); Dept. Progreso: 2 mi NE of Progreso, 14 Nov 1943, S. S. White 5109 (MICH).

PLATE XV

SCLEROCARPUS UNISERIALIS (Hook.) Benth. & Hook. f. ex Hemsl.

Fig. 1. Apex of mature plant, var. uniserialis, x 0.5,

Lindenheimer 432 (US).

Fig. 2. Maturing disk flower, var. uniserialis, x 5,

Feddema 1468 (MICH).

Fig. 3. Mature marginal receptacular bract enclosing the
achene, var. rubridiscus, x 5, Feddema 1650 (MICH).

Fig. 4. Above in longitudinal section, showing the enclosed
achene.

Fig. 5. Ray corolla, var. uniserialis, x 5, Feddema 1648
(MICH).

Fig. 6. Mature marginal receptacular bract enclosing the
achene, var. frutescens, x 5, Feddema 1501 (MICH).

Fig. 7. Above in longitudinal section, showing the enclosed
achene.

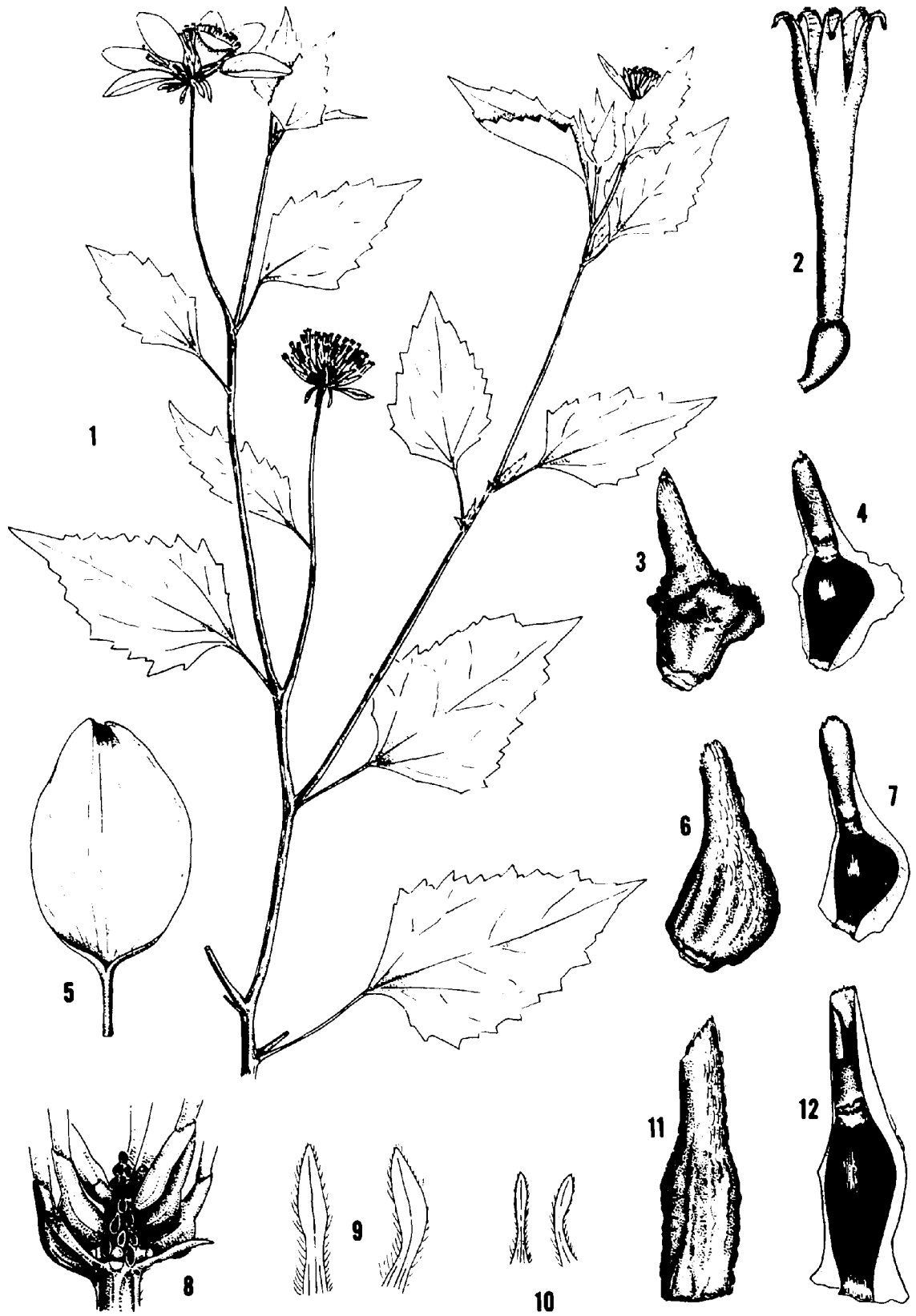
Fig. 8. Mature receptacle with one involucre bract and
most receptacular bracts removed, var. rubridiscus,
x 2.5, Feddema 1650 (MICH).

Fig. 9. Involucre bract, var. uniserialis, x 2.5,
Feddema 1468 (MICH).

Fig. 10. Involucre bract, var. rubridiscus, x 2.5,
Feddema 1650 (MICH).

Fig. 11. Mature marginal receptacular bract enclosing the
achene, var. uniserialis, x 5, Feddema 1468 (MICH).

Fig. 12. Above in longitudinal section, showing the
enclosed achene.



8. *SCLEROCARPUS UNISERIALIS* (Hook.) Benth. and Hook. f.,
ex Hemsl. Biol. Centr. Am. Bot. 2:164. 1881. Plate XV.

Erect annual, occasionally long-lived, the branches usually ascending, often surpassing the terminal capitulum, the upper short, the lower long, the lowest sometimes procumbent; leaves very variable in size, (1-) 3-6 (-20) cm long, including the petioles, the principal cauline ones large with petioles mostly $1/2$ to nearly as long as the blade, soon dying, upper leaves of the stem and branches smaller, the petioles mostly less than $1/3$ as long as the blade; blades mostly ovate-trullate, rarely linear-lanceolate or ovate-deltoid, scabrous or sparsely strigose adaxially, gray green and more densely strigose abaxially with longer hairs, the margin dentate or serrate with mostly coarse teeth, rarely entire, the apex acute-acuminate, rarely rounded, the base cuneate or attenuate, rarely obtuse, sometimes narrowly decurrent on the petiole; heads one to numerous, 7-25 mm high on long peduncles, these naked or with one or more reduced, leafy bracts; receptacle long-conoid, the apex pointed, the pits with raised margins; involucre uniseriate, campanulate when young, sometimes reflexed in age; involucral bracts 5-9 (-12), mostly oblanceolate, sometimes oblique, the apex acute, the adaxial surface mostly sparsely scabrous-strigose, the abaxial surface mostly with longer, appressed hairs; ray flowers 5-6 (-9), mostly yellow orange, (6-) 10-20 (-35) mm long, including the tube, spreading to a radius of 3.5 cm from the center of the disk; ligules 3.5-30 mm long, 2-17 mm

wide, slightly bent from the tube, ovate or subcircular, the apex with 2-3, mostly shallow teeth, the tube $1/5-1/2$ as long as the ligule; ray achenes 0.4-3.2 mm long, greenish, fleshy, linear or slightly arcuate when living, sometimes shriveling when dry, the apex remaining broader; disk flowers (5-) 15-40 (-50), the corolla 6-13 mm long, yellow, 0.3-1.0 mm diameter, short-pubescent basally, yellow or brownish red, 1-2.8 mm diameter at the lobes with longer appressed yellow or reddish hairs; lobes of the disk corolla 2-4.5 mm long, the outer surface yellow, reddish or with a purplish band, the apex strongly recurved or reflexed with stiff yellowish or brownish bristles projecting beyond the apical margin, the inner surface short yellow-papillate apically and with longer thin-walled yellowish or purplish hairs above the middle of the lobe; receptacular bracts green or red in bud; mature marginal sclerocarps beaked, green, brownish, purplish black or mottled, the surface with a few prominent longitudinal ribs or variously tubercled, strigose with white or brownish hairs, especially on the base of the beak and the upper part of the body; achenes of the marginal sclerocarps 3-6 mm long, including the pappus, slightly laterally compressed, elliptic-fusiform or obliquely obovate in lateral outline, narrowed to base and apex, the pappus usually consisting of a crown of fused bristles, this sometimes elongated abaxially or adaxially or reduced laterally to appear as one or more scales; chromosome number, $n = 12$.

KEY TO THE VARIETIES OF *SCLEROCARPUS UNISERIALIS*

Receptacular bracts green in bud or red only on the distal margin; mature sclerocarps of the marginal row of disk flowers striate or with numerous low, uniform tubercles; involucre bracts mostly more than 5 mm long; plants mostly more than 5 dm tall.

Mature marginal disk achenes fusiform or elliptic in lateral outline; mature sclerocarps of the marginal row of disk flowers cylindrical-conoid, the beak gradually reduced from the body and not bent from it or only scarcely so, the surface mostly tubercled; juvenile abaxial pubescence of the leaves mostly white.

Southeastern Texas.....8a. var. uniserialis p. 112

Mature marginal disk achenes obliquely obovate in lateral outline; mature sclerocarps of the marginal row of disk flowers somewhat laterally compressed, the beak sharply reduced from the body and strongly bent from it; the surface mostly striate; juvenile abaxial pubescence of the leaves mostly yellow. Eastern Mexico from Coahuila to Quintana Roo, Oaxaca, Chiapas and northeastern

Guatemala.....8b. var. frutescens p. 119

Receptacular bracts purplish or brownish red in bud; mature sclerocarps of the marginal row of disk flowers with a few large, complex tuberculate swellings about the middle; involucre bracts mostly less than 5 mm long; plants mostly less than 5 dm tall. Guerrero and Morelos, with

related plants or introgressants in eastern Michoacan,
Puebla and southern Oaxaca....8c. var. rubridiscus p. 126

8a. *SCLEROCARPUS UNISERIALIS* (Hook.) Benth. & Hook. f. ex
Hemsl. var. *UNISERIALIS*.

Gymnopsis uniserialis Hook. Icones Plantarum 2:t. 145.

1837. Type: TEXAS: Austin Co., San Felipe, Drummond
135 "bis...Texas II" (Holotype K!; isotypes GH!
K! NY!).

Aldama uniserialis (Hook.) A. Gray, Journ. Boston Soc.

Nat. Hist. 6:228. 1850. Type: TEXAS: Bexar Co.,
Comale Creek, 1847-1848, Lindheimer 432 (Holotype NY!;
isotypes F! GH! MO! NY! US!).

Sclerocarpus major Small, Fl. Southeastern U.S. 1250.

1903. Type: TEXAS: Bexar Co., Comale Creek, 1847-
1848, Lindheimer 432 (Holotype NY!; isotypes F! GH! MO!
NY! US!).

Plants somewhat coarse, (0.1-) 1-2 (-2.5) m tall, the
stem somewhat woody at base in age, usually much-branched;
pubescence of the stem and branches whitish with hairs to
1.5 mm long; leaves (1-) 3-6 (-17) cm long, the petioles
(1/6-) 1/4-1/3 (-1/2) as long as the blade; blades ovate-
trullate or rhombic, rarely deltoid, (1-) 3-5 (-13) cm long,
(1-) 2-4 (-8) cm wide, the margin with (2-) 3-8 (-16)
irregular, mostly sharp teeth on each side, the adaxial
surface strigose-scabrous with hairs to 1.0 mm long, the
abaxial surface with whitish or yellowish hairs to 1.5 mm
long; heads few to many, on peduncles to 15 cm long;
receptacle (2-) 3-5 (-8) mm long, (1-) 2-4 mm diameter,
glabrous, the pits shallow, ovate-rhombic, with raised
margins; involucre campanulate in bud, spreading or somewhat

reflexed at maturity, sometimes strongly reflexed in age, often with one or more bracts to 35 mm long at the base of the involucre or on the peduncle; involucral bracts subtending the ray flowers conspicuous, unequal, oblanceolate-spatulate, rarely elliptic, sometimes oblique or asymmetric, (3-) 5-10 (-15) mm long, (0.5-) 1-2 (-5) mm wide, sparsely short-scabrous adaxially, with hairs to 1.8 mm long abaxially, the margins ciliate; ray flowers 5-6 (-8), (7-) 10-20 (-35) mm long, including the tube, spreading to a radius of 3.3 cm from the center of the disk, the tube 3-8 mm long, $1/5-1/2$ as long as the ligule, the ligule yellow or orange, (3.5-) 10-15 (-30) mm long, (2-) 4-12 (-17) mm wide; disk flowers (5-) 12-50, oriented in the head to form nearly a hemisphere, the marginal ones nearly perpendicular to the surface of the receptacle; disk corollas 7-13 mm long, yellow or greenish, 0.3-1 mm diameter at base, yellow or red, short-pubescent, 1.0-2.3 mm diameter below the lobes; lobes of the disk corolla 2.5-5 mm long, the outer surface yellow with light or yellowish hairs and bristles or occasionally red with a yellow apex, and red or reddish hairs and bristles, the inner surface yellow, long-papillate apically, red or yellow below with a light colored beard above the middle of the lobe; anthers rarely exserted from the corolla tube; young receptacular bracts green or reddish purple distally; mature marginal sclerocarps 6-10.5 mm long, inserted nearly perpendicular to the surface of the receptacle, the body 1.5-3 mm diameter, cylindrical or conoid, mostly narrowing

gradually to the beak, sometimes slightly laterally compressed and rhombic in cross-section, usually widening at the attachment; surface of the sclerocarp greenish, straw-colored, grayish brown or purplish, rarely dark-mottled, somewhat strigose with white hairs to 0.7 (-1) mm long, usually with a few low longitudinal ribs, often with low rounded tubercles on the ribs or scattered on the beak; mature marginal achenes (3-) 4-6 mm long, 1.4-2.8 mm measured radially, slightly oblique, narrowly ellipsoid-obovoid or fusiform, narrowing to the base, sometimes widening at attachment; pappus mostly 0.2-0.5 mm long, usually longest abaxially and adaxially, occasionally reduced to scales there connected by a low yellowish ring, rarely reduced to a single scale; chromosome number, $n = 12$ (Feddema 1468, MICH).

Southeastern Texas at elevations from sea level to 250 meters, flowering April to December.

The disk corollas in this variety exist in two conspicuously different color forms. Specimens from Duval, Jim Hogg, Brooks, Starr, Hidalgo and Willacy Counties and most specimens from Kenedy County have disk corollas that are dark brownish red from near the middle of the tube to just below the apex of the lobe. Specimens from elsewhere in Texas appear to have all yellow corollas although this cannot be ascertained beyond doubt as the red color may have faded in some older specimens. A specimen from Kenedy County, M. C. Johnston 53.280.40 (TEX), has one head with

red disk corollas and another with yellow ones, suggesting that in this area the red form has its northern limit.

Specimens examined having red disk corollas;

DUVAL CO.: 3 mi E of Bruni, 10 Nov 1962, María Solís 32 (TEX).

KENEDY CO.: Norias Div. of King Ranch, 23 Jul 1953, M. C. Johnston 53.280.40, 24 Nov 1953, Johnston 53.280.43, 27 Sep 1953, Johnston 53.280.42 (TEX).

BROOKS CO.: Falfurrias, 16 Jul 1925, B. C. Tharp 3836 (TEX, US); between Encino and the carbonblack plant, 16 Apr 1954, Johnston 54505 (TEX); 5 mi N of Encino, 22 Sep 1961, Feddema 1468 (MICH); S of Falfurrias, 15 Sep 1942, C. Lundell 11946 (MICH); King Ranch, Encino Div. Headquarters, 13 Nov 1954, Gould & Morrow 6759 (TEX); Falfurrias, 13 Nov 1940, H. B. Parks 1954 (TEX), Parks 1955 (MO), 10 Sep 1940, Parks 1153, 2594 (MO); Falfurrias, 8 Jun 1935, V. L. Cory 14785.

JIM HOGG CO.: 3 mi W of San Isidro on road 1017, 9 Oct 1954, Tharp & Johnston 541861 (TEX).

HIDALGO CO.: 10.8 mi N of San Manuel, 4 Aug 1961, Feddema 1487 (MICH); N of Edinburg, 11 Nov 1942, M. L. Walker 128 (GH, TEX); 35 mi N of Edinburg, 23 Aug 1944, E. Whitehouse 44.278 (GH).

STARR CO.: 25 mi above Rio Grande City, 16 Jun 1928, Tharp (TEX).

WILLACY CO.: Raymondville, 4 Jul 1941, I. Shiller 757 (US); Yturria Station, 8 May 1937, R. Runyon 1686 (US);

2.4 mi S of Yturria, 6 Jul 1954, Johnston 541090 (TEX);
Yturria, 15 Jul 1940, Runyon 2390 (F).

Specimens examined, all apparently having yellow disk
corollas:

WILLIAMSON CO.: Georgetown, 12-19 Oct 1897, E. Palmer
595 (NY).

TRAVIS CO.: Austin, 30 Jul 1882, G. W. Letterman (MO, NY,
TEX, US); 14 Nov 1939, B. H. Warnock 75 (TEX); Colorado
River, Austin, 8 Oct 1941, B. C. Tharp 96 (GH, MO); Austin,
8 Oct 1891, J. E. Bodin 186 (US); near Univ. of Texas, 29
Sep 1908, York & Wolf 41 (TEX).

BASTROP CO.: Bastrop, 9 Sep 1903, Biltmore Herbarium
14870c (US); Piney Creek, 3 Oct 1928, H. H. Duval 147 (TEX).

HAYS CO.: San Marcos and vicin. S. W. Stanfield (NY).

COMAL CO.: Comanche Spring, New Braunfels 1849-1851,
Lindheimer 957 (F, GH, MO, NY, TEX, US).

BEXAR CO.: "Bejar", Aug 1828, Berlandier 1850 (K); San
Antonio, Sep 1887, G. Bell 759 (MO); San Antonio, E. H.
Wilkinson 5 (MO); San Antonio, G. Jermy 57 (NY), Jermy 86
(MO, US); San Antonio, 2 Oct 1900, B. F. Bush 1206 (MO, NY,
US); San Antonio, 5 Sep 1920, E. D. Schulz 189 (US); Cibolo
River, near Bracken, 11 Jul 1903, H. A. Groth 84 (F, GH, NY,
US); San Antonio, 1897, E. H. Wilkinson (MO); near Cibolo
Creek, 7-9 Oct 1887, Schott 561a (GH, NY).

GUADALUPE CO.: Staples, 7 Sep 1930, Whitehouse (MICH, NY,
TEX).

GONZALES CO.: Kornstad's farm, near Ottine, 3 Oct 1934,
Whitehouse 12114 (MICH); Ottine, 3 Oct 1943, Tharp, Brady &

Barkley 13959 (F, MO, TEX); Ottine Swamp, 27 Sep 1934,
Cory 10129 (GH); Ottine, 31 Oct E. R. Bogush 967 [1017?]
 (TEX).

FORT BEND CO.: Rosenberg, 25 Sep 1914, Palmer 6641 (F,
 MO, US).

BRAZORIA CO.: Columbia, 5 Oct 1900, B. F. Bush 1280 (MO,
 NY); Columbia, 30 Sep 1907, Bush 954 (MO).

WILSON CO.: Kicaster School, 2 Sep 1940, Parks 1515
 (MO); Cover Ranch, 26 Sep 1940, Parks 1442 (MO).

JACKSON CO.: 3 mi S of Vanderbilt, 16 Sep 1953, Turner,
Tharp, Johnston 53-393 (TEX); Menehee Flats, S of
 Vanderbilt, 26 Nov 1943, Tharp & Barkley 13A158 (MO, TEX);
 Lavaca River, 29 Aug 1941, B. C. Tharp (TEX).

KARNES CO.: Escondido Creek, 2.5 mi N of Kenedy, 23 Oct
 1952, J. C. Johnson 1074 (TEX).

VICTORIA CO.: Da Costa School, 23 Oct 1927 (collector
 not known 6520)(TEX).

REFUGIO CO.: approx. 10 mi N of Refugio, 13 Oct 1963,
Feddema 2116 (MICH); 2.5 mi S of Refugio, 13 Oct 1963,
Feddema 2117 (MICH).

SAN PATRICIO CO.: N shore of Nueces Bay, 1 mi W of
 projected end of NS road 893, 10 Dec 1960, A. Traverse
1791 (TEX).

BEE CO.: near Papalote, 11 Aug 1946, C. C. Albers 46336
 (F, TEX).

ARANSAS CO.: Aransas Refuge, 27 Sep 1879 - Oct 1880,
Palmer 594 (GH, MO, NY, US); North Beach, Corpus Cristi,
 7 Aug 1921, Ferris & Duncan 3227 (MO, US); vicin. Corpus

Cristi, 24 Oct 1913, J. N. Rose 18068 (NY, US); near Corpus
Cristi, Mar 1894, A. A. Heller (NY).

KLEBERG CO.: Loyola Beach, Riviera, 15 Oct 1948, Bogush
Sl72 (US); Laguna Madre, Laureles Div. of King Ranch, 15
Sep 1953, Johnston 53.280.25 (TEX); Laguna Madre, E of
Mortilla camp house, Laureles Div. of King Ranch, 3 Jul
1953, Johnston 53.280.41 (TEX).

8b. *SCLEROCARPUS UNISERIALIS* (Hook.) Benth. & Hook. f.var. *FRUTESCENS* (Brandg.) Feddema, comb. nov.*Sclerocarpus frutescens* Brandg. Univ. Calif. Publ. Bot.4:281. 1912. Type: SAN LUIS POTOSI: between Bagre and Minas de San Rafael, Jul 1911, C. A. Purpus 5157 (Holotype UC; isotypes F! GH! MO!).

Erect annual, variable in form, (0.2-) 0.3-1.0 (-1.5) m tall, sometimes long lived and persisting well into the second growing season with the base of the stem and root much-thickened and adventitious roots and ascending branches arising from the base of the stem and lower branches, the pubescence of whitish or often yellowish, bulbous-based hairs mostly less than 1 mm, rarely to 2 mm long; leaves (2-) 3-8 (-13) cm long, including the petioles, these mostly $1/5$ - $1/3$ as long as the blade; blades mostly narrowly lanceolate-trullate, sometimes ovate-trullate, rarely linear-lanceolate or broadly ovate, (1-) 2-5 (-10) cm long, (0.2-) 0.5-2.5 (-6) cm wide, scabrous-strigose adaxially with mostly white hairs less than 1 mm long, strigose or rarely strigose-pilose abaxially with white or yellowish hairs to 1.6 mm long, the pubescence often yellow on young leaves, the apex mostly acute-acuminate, the margin shallowly dentate-serrate or coarsely dentate with (2-) 4-6 (-12) regular or irregular teeth on each side, rarely entire; heads few to several, 8-19 mm high; receptacle (2-) 3-5 (-9) mm long, 1-5.5 mm diameter, glabrous, involucre often reflexed at maturity, the bracts 5-9, (3-) 4-8 (-13) mm long, 0.5-1.5 (-3) mm wide, mostly

linear-lanceolate to oblanceolate, rarely lanceolate-elliptic; ray flowers 5-7 (-9), mostly yellow, occasionally yellow orange, (6-) 9-15 (-23) mm long, including the tube, spreading to a radius of 2.5 cm from the center of the disk, the tube mostly $1/4$ - $1/3$ ($-1/2$) as long as the ligule, the ligule 6-20 mm long, 4-12 mm wide, narrowly to broadly ovate or subcircular; disk flowers 15-40, oriented in the head to form an inverted cone including an angle of approximately 30-50 degrees, the corollas yellow orange, sometimes greenish at base, 0.3-0.8 mm diameter at base, 0.7-2.2 mm diameter at the lobes; lobes of the disk corolla 2-3.5 mm long, the outer surface yellow or with a purple area above the middle, the pubescence yellow or brownish with a few apical bristles, the inner surface with thin-walled hyaline or purple hairs above the middle of the lobe, these projecting beyond the margin of the lobe and often forming a purplish band about the corolla above the middle of the lobes; mature marginal sclerocarps 5-8 (-9) mm long, green, grayish brown, rarely purplish black or mottled, somewhat strigose, with a few low longitudinal ribs, mostly without tubercles or rarely with numerous small uniform tubercles, the body perpendicular to the surface of the receptacle, 1-2 mm measured radially at base, widening above and narrowing sharply to the beak, the beak approximately 1 mm diameter, nearly as long or longer than the body and somewhat bent from it; receptacular bracts of the central disk nearly tubular; achenes of the marginal sclerocarps 3.2-4.6 mm long, including the pappus, approximately 2.5 mm

measured radially, considerably oblique in lateral outline, narrowed to base, sharply narrowed to the pappus, the pappus 0.2-1.1 mm long; chromosome number, $n=12$ (Feddema 1502, MICH).

Southeastern Coahuila, Nuevo Leon, southern Tamaulipas, San Luis Potosi, Hidalgo, Guanajuato, Mexico, Vera Cruz, eastern Oaxaca, Campeche, Yucatan, Quintana Roo, Chiapas and northeastern Guatemala, at elevations from sea level to 2700 meters, usually flowering from March to September but capable of persisting into the second year.

This variety is somewhat intermediate in form between the other two. It is isolated geographically from var. uniserialis but hybridizes with var. rubridiscus where their ranges overlap. It is distinguishable from the former by its shorter, strongly-bent marginal receptacular bracts, and from the latter by its longer involucre bracts, its green receptacular bracts and its thinner sclerocarps with only ribs or small tubercles.

Specimens examined:

COAHUILA: Múzquiz-La Mariposa, 5 Dec 1936, E. Marsh 1028 (F, TEX); 40 km N of Monclova, 24 Aug 1961, Feddema 1823 (MICH); Soledad, 25 mi SW of Monclova, 9-19 Sep 1881, E. Palmer 596 (NY, US); Puerta de San Lázaro, Munic, Castaños, 31 Aug 1939, C. H. Mueller 3019 (F, GH, MICH); 20 km ESE of Cuatro Ciénegas, 25 Mar 1941, A. H. Schroeder 116 (GH); 37 mi S of Monclova, 2 Aug 1961, Powell & Edmondson 506 (MICH, TEX).

NUEVO LEON: Monterrey, 20 Jun 1888, C. Pringle 1900 (F, GH, NY, US); Canyon above El Diento, Monterrey, Oct 1961, R. F. Smith M564 (TEX); Cola de Caballo, Monterrey, 17 Sep 1959, C. Diaz (MICH); Horestail Falls, S of Monterrey, 7 Sep 1962, Turner & Powell 1026 (TEX); 35 mi S of Monterrey, 27 Jun 1939, S. S. White 1589 (GH, MICH); Galeana, 30 Jul 1939, V. H. Chase 7668 (F, GH, MICH, MO); Alamar, 15 mi SW of Galeana, 1 Jun 1934, C. H. & M. T. Mueller 441 (A, GH), 669 (TEX); 8 mi N of Escondido [Escondida], 27 Aug 1940, Shreve & Tinkham 9716 (GH).

TAMAULIPAS: between Victoria and Antiguo, 20-23 Jun 1937, G. H. Happ 33 (MO); 12 mi SW of Antiguo, 22 Aug 1956, Fearing & Thompson 186 (TEX); 19 mi SE of Miquihuana, 11 Aug 1941, Stanford, Retherford, Northcraft 832, 832a (GH, MO, NY); Jaumave, 1930, H. W. Viereck (US); vicin. Gómez Farfías, 13-21 Apr 1907, E. Palmer 280 (F, GH, MO, NY, US); 29 mi N of Ciudad Mante, 4 Aug 1961, Feddema 1489 (MICH); 18 mi NW of Ocampo, 23 Aug 1941, Stanford, Retherford, Northcraft 1073 (GH, MO, NY); Ocampo, 30 Aug 1948, Kenoyer & Crum 3585 (MICH); 2 mi E of Altamira, 2 Mar 1961, R. King 4086 (F, MICH, NY, TEX, US); vicin. Tampico, Jan 1910, Palmer 62 (MO, US); 22.5 mi NE of Manuel, 14 Sep 1956, Martinez & Luyando F1629 (TEX); 11 mi N of Manuel, 10 Dec 1959, M. C. Johnston 4935A (TEX).

SAN LUIS POTOSI: Aquismon, 2 Mar 1959, J. Rzedowski 10194 (MICH); region of San Luis Potosí, 1878, Parry & Palmer 467¹/₂ (GH, NY); 30 mi E of San Luis Potosí, 6 Nov 1960, Crutchfield & Johnston 6032A (TEX); Sierra de Alvarez,

ca. 40 km ESE of San Luis Potosí, 19 Sep 1963, R. McVaugh 22160 (MICH); Minas de San Rafael, Nov 1910, C. A. Purpus 4767 (F, GH, MO, US); 15 mi E of Ciudad del Maíz [Ciudad Maíz], 1 Aug 1960, J. T. Mikel 529 (MICH); 15 mi E of Ciudad de Maíz [Ciudad Maíz], 29 Aug 1947, Barkley, Webster, Paxon 859 (TEX); 20 mi E of Ciudad del Maíz [Ciudad Maíz], 23 Jul 1953, W. E. Manning 53455 (GH); Micos, 19 Jul 1933, G. L. Fisher 3331 (US); 21 km N of Valles, 4 Aug 1961, Feddema 1501 (MICH); 14 mi N of Valles, 14 Sep 1959, J. Graham & M. C. Johnston 4008A; Valles, 18 Jul 1933, R. A. Vines 3314 (US); Rascon, Aug 1911, Purpus 5246 (F, GH, MO, NY, US); 36 km N of Tamazunchale, 4 Aug 1961, Feddema 1502 (MICH); Tamazunchale, Jul 1937, Lundell 7137 (MICH); Tamazunchale, 10 Jul 1937, M. T. Edwards 460 (F, TEX); vicin. Tamazunchale, 25 May 1939, T. C. Frye 2660 (GH, NY, US); near Axtla, 25 Jun 1942, J. N. Weaver 647 (GH, US); Route 85, just N of San Luis Potosí-Hidalgo border, 23 Mar 1961, King 4233 (F, MICH, NY, TEX, US); "en route from San Luis Potosí to Tampico", Dec 1878 - Feb 1879, Palmer 1104 (GH, NY, US).

GUANAJUATO: approx. 1 mi S of Ixtla, 13 Oct 1963, Feddema 2118 (MICH).

HIDALGO: Jacala, 16 Nov 1937, L. A. Kenoyer 645 (F, MO), 14 Aug 1937, M. T. Edwards 815 (F); between Huejutla and Macuxtepetla, on road to Ixcatlán, 21 May 1947, H. E. Moore Jr. 2924 (GH); Jacala, 25 Jun 1959, V. H. Chase 7121 (F, GH, MICH, MO); 4 mi S of Jacala, 4 Aug 1961, Feddema

1503 (MICH); vicin. Zimapán, 22 Jun 1947, Kenoyer 1037 (GH); Metztitlán, 24 Nov 1946, H. E. Moore 2141 (GH).

VERACRUZ: 4 mi N of Tampico, El Alto, 7 Mar 1961, King 4094 (F, MICH, NY, TEX, US); 3 mi S of Naranjos, 7 Mar 1961, King 4118 (F, MICH, NY, TEX, US); near Panuco, Apr 1888, E. Seller 687 (GH); 5 mi E of San Luis Potosí line on Valles-Tampico highway, 11 Dec 1960, Crutchfield & Johnston 6099 (MICH, TEX); vicin. Palmar, 3 Sep 1935, L. H. MacDaniels 877 (F); Laguna Tamiahua, 25 mi S of Tampico, 2 Mar 1939, LeSuer 502 (F), 504 (F, TEX); Actopán, between Jose Cardel and Palmas Abajo, 15 Feb 1943, Gilly Simpson & Dodds 111 (MICH); Puente Nacional, km 388 on Jalapa-Veracruz highway near Rinconada, 13 Feb 1943, Gilly, Simpson & Dodds 84 (MICH).

CAMPECHE: Calakmul, 31 Dec 1931, Lundell 1149 (F).

MEXICO: near San Pablo, 15 mi S of Mexico City, 16-18 Jul 1937, Happ 297 (MO).

QUINTANA ROO: Coba, Jun - Jul 1938, Lundell 7748 (A, F, MICH, TEX, US).

Specimens of var. frutescens examined, showing some characters of var. rubridiscus:

OAXACA: 10-15 km N of Tehuantepec, 26 Jul 1958, King 735 (MICH); 54 mi NW of Tehuantepec, 13 Oct 1962, R. McVaugh 21829 (MICH); 24 km NW of Tehuantepec, 8 Aug 1961, Feddema 1596 (MICH).

CHIAPAS: road from Ocuilapa to Tuxtla, 29 Aug 1895, E. W. Nelson 3070 (GH, US).

GUATEMALA: DEPT. HUEHUETENANGO: between Nentón and
Catarina, 3 Sep 1942, J. Steyermark 51808 (F); between
Santa Ana Huista and Nentón, 27 Aug 1942, Steyermark 51425
(F, US).

8c. *SCLEROCARPUS UNISERIALIS* (Hook.) Benth. & Hook. f.

ex Hemsl. var. *RUBRIDISCUS* Feddema, var. nov.

plerumque brevis, 2-6 (-15) dm alta; folia (2-) 3-4 (-9) cm longa; lamina anguste trullata (2-) 3-4 (-7) cm longa; bractee involucri lineares vel oblanceolatae, circiter 2.5-5 mm longae, 1-2 mm latae; receptaculum glabrum; marginis receptaculi paleae maturae valde curvae, 6-8 mm longae, valde turgido-tuberculatae in medio, corpore quam rostrum plerumque paullo longiore; pappus 0.3-0.9 mm longus; achaenia 4-5 mm longa.

Plants mostly small, typically 2-5 dm tall (some closely related plants to 1.5 m tall), with 1-3 short upper branches and long, procumbent or ascending lower branches, rarely the latter not developing; pubescence on older portions of the stem and branches mostly appressed, to 0.7 mm long, that of younger branches mostly 0.5-1.0 mm long, somewhat spreading; leaves typically 2-5 cm long, including the petioles, the petioles of the principal cauline leaves nearly 1/2 as long as the blades; blades (2-) 3-5 (-7) cm long, 0.5-2 (-4.5) cm wide, narrowly to broadly ovate-trullate, scabrous or sparsely strigose adaxially with whitish hairs to 0.7 mm long, strigose abaxially with whitish hairs to 1.1 mm long, the margin serrate-dentate with 1-4 (-8) regular or irregular, coarse or very shallow teeth, rarely entire or with short irregularly toothed basal lobes, the apex sometimes rounded, the base cuneate; heads one to several, 9-20 mm high, on peduncles to 14 cm

long, these naked or with one or more leafy bracts, sometimes enlarged at the receptacle; receptacle long-conoid, (3-) 5-7 (-10) mm long, 1-3 mm diameter, the apex sharp, the pits with raised margins, especially abaxially, sometimes with a few short hairs; involucre somewhat appressed to the sclerocarps in age or spreading, the bracts short, grayish green, typically 2.5-5.0 mm long, 0.8-1.7 mm wide, mostly linear-lanceolate, rarely lanceolate, somewhat shriveled and inrolled in age, sparsely strigose adaxially; ray flowers 5-6 (-7) the corolla (10-) 12-18 mm long, including the tube, the tube mostly $1/3$ - $1/2$ as long as the ligule, the ligule ovate or subcircular, 8-14 mm long, 7-15 mm wide, the achenes (0.3-) 0.7-1.2 (-1.8) mm long, 0.3-1.0 mm wide; disk flowers (15-) 20-40 (-45), oriented in the head nearly parallel to the axis of the receptacle; disk corollas 6-12 mm long, 0.5-0.9 mm diameter, yellow or greenish, yellow-pubescent at base, 1.4-1.8 mm diameter, yellow or purplish with brownish or reddish hairs below the lobes; lobes of the disk corolla 2.4-3.5 mm long the outer surface with the basal $1/2$ - $2/3$ purplish with coarse orange brown or purplish red hairs to 0.6 mm long, the distal $1/3$ yellow, glabrous except brownish bristles at apex, the inner surface short yellow-papillate at the apex with mostly purplish thin-walled hairs to 0.6 mm long below; immature receptacular bracts dark brown or purplish red in bud, coloring the disk before emergence of the flowers; mature marginal sclerocarps 5-9 mm long, the body mostly 3-4 mm long, narrow at base, sometimes rhombic in cross

section, the upper portion usually enlarged and with conspicuous rounded tubercles or complex tuberculate swellings, sharply narrowed to the beak, the beak approximately 1 mm diameter, usually shorter than the body and bent from it; achenes of the marginal sclerocarps 4-5 mm long, including the pappus, considerably oblique in lateral outline, the pappus a greenish white or yellowish tubular crown of fused bristles 0.3-1.0 mm long, the margin very irregular; chromosome number, $n = 12$ (Feddema 1710, MICH).

Guerrero, Morelos, western Oaxaca, at elevations of 600 to 2000 meters, flowering July to November.

Type: MORELOS: 6 mi S of Chilpancingo, 13 Aug 1961, Feddema 1650 (Holotype MICH).

This variety is distinct in the central portion of its range and recognizable by its low stature, the dark purplish disk on immature heads and the swollen tuberculate sclerocarps. It shows introgression with var. frutescens in the eastern part of its range where some plants have larger leaves, young heads with green receptacular bracts, sclerocarps with few or low tubercles and disk corollas which resemble those of var. frutescens in coloration. West of its range are found plants assignable to the species but of problematical varietal position. Plants growing in western Guerrero are closely related to var. rubridiscus but those in western Michoacán resemble this variety and also var. uniserialis from which it is well isolated geographically.

Specimens examined:

MORELOS: 11 km S of Cuernavaca, 11 Aug 1961, Feddema 1613, 1614 (MICH); 6 mi W of Yautepec, 14 Aug 1950, D. Pipes 82 (MICH).

GUERRERO: 10 km S of Taxco, 12 Aug 1961, Feddema 1646 (MICH); 5 km N of Iguala, 12 Aug 1961, Feddema 1647 (MICH); 35 km S of Iguala, 12 Aug 1961, Feddema 1648 (MICH); 1 mi S of Buena Vista on Mexico-Taxco toll road, 4 Nov 1960, Crutchfield & Johnson 6007 (MICH, TEX, US); mts. N of Tierra Colorado, 12 Jul 1941, Leavenworth 971 (F, MO); 7 mi W of Chilpancingo, 16 Jun 1953, Wilkinson & Rowell 3395 (MICH); 65 mi N of Acapulco, 20 Aug 1961, Powell & Edmondson 788 (MICH, TEX); Taxco Viejo, 18 Sep 1937, R. Q. Abbott 403 (GH).

Specimens examined showing close relationship to var. rubridiscus but showing various degrees of introgressive influence of var. frutescens:

PUEBLA: 29 km NW of Huajuapán, Oaxaca, 9 Aug 1961, Feddema 1611 (MICH); 2 mi SE of Tehuiztzingo, 15 Aug 1961, Powell & Edmondson 718 (MICH, TEX); 40 mi S of Tehuacan, 13 Aug 1961, Powell & Edmondson 657 (MICH, TEX).

OAXACA: 16 km SE of El Camarón, 8 Aug 1961, Feddema 1607 (MICH); El Fortín, Sep 1898, Gonzalez & Konzatti 907 (F, MICH); Cerro Juarez, 1 Sep 1907, Konzatti 1946 (GH); 49 mi W of Tehuantepec, 23 Jul 1960, R. King 3458 (MICH, NY, TEX, US); 1 mi NE of Huajuapán, 28 Jul 1960, R. King 3533 (MICH, NY, TEX, US); 3 km NW of Huajuapán, 9 Aug 1961, Feddema 1610 (MICH); 1 mi N of Tamazulapán, 20 Jun 1960, King 2936

(MICH, NY, TEX, US); 6 mi E of Oaxaca, 14 Aug 1961,
Powell & Edmondson 690 (MICH, TEX).

Specimens examined which have some characters of var.
rubridiscus, but departing to a lesser or greater extent
from the characters of the typical plant of this variety:

MICHOACAN: 8 km SW of Nueva Italia, 15 Aug 1961, Feddema
1710 (MICH); Barranca de Jungapen, Oct 1907, L. Digue
(MICH); Tacupa, Dist. Huetamo, 18 Jan 1934, G. Hinton 5504
(F, GH, K, MO, US); Zitácuaro, Las Anonas, 23 Aug 1938,
Hinton 13144 (GH, MICH, US).

GUERRERO: Coyuca, 26 Jan 1934, Hinton 5550 (F, GH, K,
MO, NY, US); Pungarabato, Dist. Coyuca, 9 Jan 1934, Hinton
5441 (GH, K).

EXCLUDED SPECIES

1. SCLEROCARPUS DISCOIDEUS Vatke, Linnaea 39:495. 1875.

Siegesbeckia discoidea (Vatke) Blake, Contr. U.S.
Nat. Herb. 26:244. 1930.

Blake (1930), discussing the propriety of referring this plant to Sclerocarpus, reviewed the history of this species. Vatke, when publishing the name, cited in synonymy Guizotia discoidea which had been published by Shultz Bipontinus without characterization and only mentioning a collection of Schimper in 1850 at Debra-Eski. Vatke did not refer to this collection but based his name on Schimper 529 from Monte Arba Tensesa [Tenesa] collected in 1862. Blake examined an isotype of this collection and believed the specimen to be neither assignable to Sclerocarpus or Guizotia but placed it in Siegesbeckia and made the above combination. An examination of an isotype from the Herbarium of The Royal Botanic Garden at Kew, confirms Blake's contention that this plant is not a species of Sclerocarpus. It is also plainly not assignable to Aldama.

2. SCLEROCARPUS EXIGUUS Smith in Rees, Cycl. 33. 1815.

Madia exigua (Smith, in Rees) A. Gray, Proc. Am. Acad.
8:391. 1873.

3. SCLEROCARPUS GRACILIS Smith in Rees, Cycl. 33. 1815.

Madia gracilis (Smith, in Rees) Keck, Madroño 5:169.
1940. [Madia dissitiflora (Nutt.) Torr. & Gray,
Fl. N. Amer. 2:405. 1843.]

As related by Keck (1940), Dr. J. Clausen discovered an isotype of Sclerocarpus gracilis at Kew and identified it as the species which had been known as Madia dissitiflora T. & G. Keck also stated that Dr. I. W. Wiggins examined both the type of Sclerocarpus gracilis and S. exiguus in James Edward Smith's herbarium at the Linnean Society of London and made photographs. Keck made the transfer of S. gracilis to Madia and expressed agreement with Gray's disposition of S. exiguus. Keck's views of the two species are accepted by Munz (1959), and Abrams and Ferris (1960).

ALDAMA La Llave & Lexarza, Nov. Veg. Descr. 14. 1842.

Gymnopsis DC. Prodr. 5:461. 1836. (In part).

Sclerocarpus (Of authors, in part).

Erect, rarely ascending, herbaceous annuals, occasionally persistent, with the base of the stem and root thickened and woody; stem terete, green or purplish red, somewhat striate, glabrate on older and basal portions, mostly strigose-hispidulous with the hairs subappressed on younger branches and peduncles; lower branches opposite, decussate, long, procumbent or ascending; leaves 3-nerved, the principal cauline ones large with petioles mostly less than 1/4 as long as the blades, dying on the mature plant, those of the upper stem and branches reduced, the petioles shorter in proportion to the blade; blades mostly lanceolate, substrigose, dark green adaxially, paler green and glandular-dotted abaxially with shorter hairs, especially between the prominent veins, the apex mostly acute-acuminate, the base cuneate or rounded, the margin mostly shallowly serrate; heads several to numerous, radiate, mostly long-peduncled, terminal on the stem and branches or in twos or threes terminally or axially; receptacles chaffy, mostly low-convex when living or becoming ovoid-conoid or subglobose after the fall of the receptacular bracts; involucre biseriate or appearing triseriate, campanulate when young, closely appressed to the disk flowers and concealing the maturing receptacular bracts, the apex sometimes spreading, the entire bract sometimes spreading in age; involucral bracts 10-17, green, imbricate, graduate, somewhat stiff, becoming

somewhat chaffy and sometimes brownish in age, the inner often scarious along the basal margins; ray flowers neutral, ligulate, the tube mostly $1/7-1/5$ as long as the ligule; ligules yellow or yellow orange, linear-oblong or narrowly ovate, turning red at base in sodium or potassium hydroxide solutions, the apex 2-3 toothed, yellow glandular-dotted and minutely strigulose on the veins abaxially, the achenes hollow, thin-walled, triangular in cross section, arcuate, persisting on the receptacle, flattened and membranaceous when dry, the apex remaining broad; disk flowers perfect, short, 10-nerved, the tube mostly $1/3-1/2$ as long as the tube, the lobes mostly less than 1.2 mm long, the inner surface entirely short-papillate; anthers exserted from the corolla tube at anthesis, the connective broadly lanceolate or ovate-deltoid, mostly less than twice as long as wide, the base short-sagittate; stigmatic arms somewhat flattened, the non-stigmatic hairs outside mostly short except long in a tuft below the apex; mature receptacular bracts enclosing the achenes and falling with them, those at the margin of the disk slightly surpassing the achene, narrowed apically into a low, irregular or toothed rim, the apex of the achene visible in the neck of the enclosing bract; the wall of the mature bract thin, brittle, membranaceous, with an inner membrane appressed to the achene and an outer membrane irregularly evaginated or inflated to form coarse longitudinal and transverse corrugations and pits and frequently wing-like ribs laterally, the inter-membrane space pithy or with air

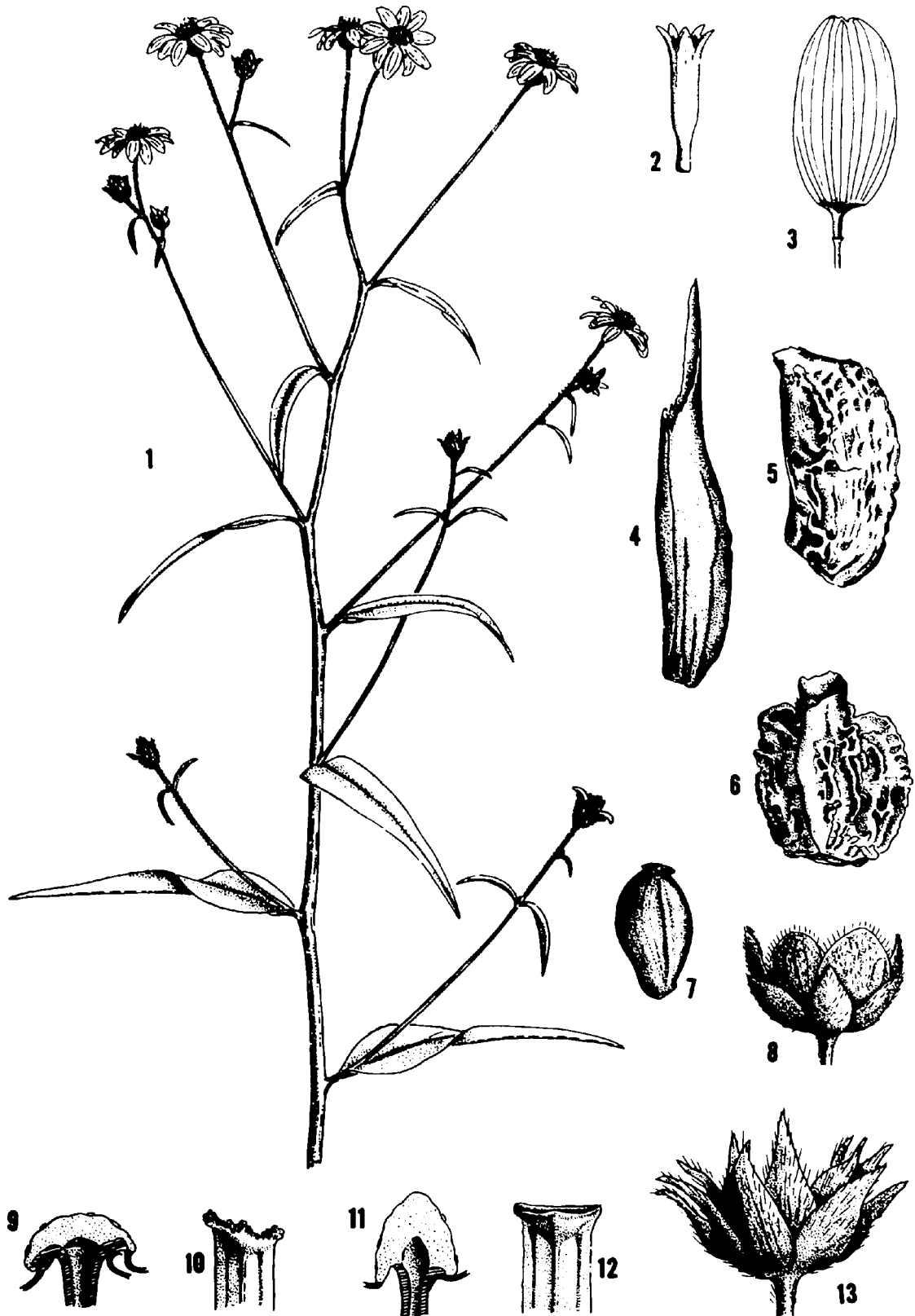
spaces containing branched, hypha-like filaments of cells; bracts of the central disk longer and narrower than those of the margin, loosely enclosing the achene, the surface smooth, the beak longer or developing a long tooth or awn often extending beyond the corolla; achenes black, minutely striate shining or grayish, those of the margin laterally compressed or radially compressed and subtriangular in cross section, those of the central disk laterally compressed, longer than those of the margin or frequently not developing; pappus a very low crown of erect or spreading fused bristles or scales, sometimes a low ridge or absent; chromosome number, $n = 17$. Type species: Aldama dentata La Llave & Lexarza.

After its proposal in 1824, the genus Aldama had little acceptance as it was soon merged by DeCandolle in his new Gymnopsis. It remained there, in spite of some disagreement as to its proper status, until Bentham and Hooker (1881) placed it in synonymy with Sclerocarpus where it has remained until the present.

PLATE XVI

ALDAMA DENTATA La Llave & Lexarza

- Fig. 1. Upper portion of plant, var. zamorensis, x 0.5
(drawn from plant grown in The University of Michigan
Botanical Gardens, from seeds of Feddema 1724 (MICH).
- Fig. 2. Disk corolla, var. dentata, x 5, Feddema 1541
(MICH).
- Fig. 3. Ray corolla, var. dentata, x 2.5, Feddema 1666
(MICH).
- Fig. 4. Receptacular bract of the central disk, var.
dentata, x 10, Feddema 1541 (MICH).
- Fig. 5. Laterally compressed marginal receptacular bract,
lateral view, var. zamorensis, x 10, Feddema 1724 (MICH).
- Fig. 6. Radially compressed marginal receptacular bract,
var. dentata, x 10, Feddema 1556 (MICH).
- Fig. 7. Radially compressed marginal disk achene, var.
dentata, x 10, Feddema 1556 (MICH).
- Fig. 8. Involucre, var. dentata, x 2.5, Feddema 1698 (MICH).
- Fig. 9. Longitudinal section through dry receptacle, var.
dentata, x 5, Feddema 1556 (MICH).
- Fig. 10. Apex of ray achene, showing pappus, var. dentata,
x 25, Feddema 1541 (MICH).
- Fig. 11. Longitudinal section through dry receptacle, var.
zamorensis, x 5, Feddema 1724 (MICH).
- Fig. 12. Apex of ray achene, var. zamorensis, x 25,
Feddema 1724 (MICH).
- Fig. 13. Involucre, var. zamorensis, x 2.5, Feddema 1724
(MICH).



1. ALDAMA DENTATA La Llave & Lexarza, Nov. Veg. Descr.

1824. Plate XVI.

Plants somewhat coarse, very rarely procumbent, (0.3-) 0.7-1.5 (-2.5) m tall, the stem and taproot often somewhat woody in age, the plant sometimes then represented only by the base of the stem and one or more procumbent basal branches, these often rooting at the nodes; pubescence of the stem and branches various, mostly strigose-hispidulous or strigose-pilose, the hairs subappressed or erect, coarse or slender-attenuate 0.7-1.5 (-3.0) mm long, occasionally these types intermixed with very short crisped hairs, pubescence most dense below the involucre; leaves (1-) 4-8 (-14) cm long, including the petiole, this 2-15 mm long, mostly $1/10$ - $1/7$ as long as the blade, ciliate-hispidulous, often slightly margined; blades (0.5-) 1-3 (-4) cm wide, narrowly linear-lanceolate or ovate-lanceolate, rarely ovate, those of the upper stem and branches mostly narrow, those of the lower branches broader in age, the apex acute-acuminate, rarely rounded, the margin mostly shallowly serrate, with glandular, sometimes minute teeth, rarely coarsely serrate or appearing entire, usually scabrous-strigose or strigose-hispidulous with subappressed hairs to 1.8 (-2.5) mm long, the hairs abaxially longest and more spreading on the veins; heads (3-) 6-10 (-13) mm tall, on peduncles mostly 3-7 (-13) cm long; receptacle (1-) 2-4 (-5) mm diameter, mostly 1-2 mm high, brownish pitted; involucre (3-) 5-9 (-12) mm diameter, mostly 4-7 (-9) mm high; outer involucral bracts 5 (-7), (3-) 5-9 (-10) mm

long, 1-3.5 mm wide, narrowly elliptic, lanceolate, or ovate, the apex acute-acuminate, rarely obtuse, sometimes spreading, the margin ciliate, mostly scabrous-strigose abaxially, sometimes with coarse, suberect white or yellow hairs to 2.8 mm long, often with dark green or brownish markings, especially along the veins and apical margin, glabrous abaxially, whitish basally; inner involucral bracts mostly equal in number to, and subtending the ray flowers, usually longer and wider than the outer bracts, narrowly to broadly elliptic, ovate-lanceolate or obovate-ob lanceolate, the apex acute-acuminate, obtuse or rounded, the exposed surface similar in color to the outer bracts, the hairs sometimes fewer and shorter, the lower portion whitish, glabrous, the margin ciliate, sometimes scarious; ray flowers 5-7 (-11), the ligule (2.5-) 8-13 (-18) mm long, (2.5-) 4-7 (-11) mm wide, the apex mostly shallow toothed, the achenes 2-4 mm long, eppapose or with fimbriate, membranous scales to 0.3 mm long on the angles; disk flowers (8-) 20-70, the corolla (2.5-) 4-6 mm long, yellow orange, sometimes slightly reddish below the lobes, the tube mostly less than 0.5 mm diameter, the throat 0.5-2.2 mm diameter, sparsely pubescent, the lobes yellow within and without or weakly reddish on the margins; mature marginal receptacular bracts 2.4-3.5 mm long, sometimes laterally compressed, 0.7-1.5 mm wide, to 2 mm measured radially, obliquely oblong-obovate in lateral outline, strongly curved to the apex, sometimes the bract radially compressed and nearly as broad as long, trigonous in cross

section and with lateral wings, the surface greenish, brown, purplish or mottled, mostly glabrous, shallowly wrinkled or coarsely corrugate with prominent ridges and deep pits; bracts of the central disk to 8 mm long, tubular or laterally flattened, the apex mostly with a long blade or tooth abaxially; achenes of the marginal disk flowers (1.7-) 2.3-3.5 mm long, radially compressed and obovoid-trigonous or laterally compressed and obliquely obovate in lateral outline, the base narrowed and recurved, the pappus mostly less than 0.1 mm long, or absent, sometimes with a short scale or tooth abaxially or adaxially on central achenes.

KEY TO THE VARIETIES OF ALDAMA DENTATA

Apex of the inner involucral bracts narrowly acute or strongly acuminate; peduncles mostly strigose-pilose with appressed or spreading whitish hairs mostly less than 1.5 mm long; mature receptacular bracts greenish, stramineous, or light brown.....la. var. dentata p. 142

Apex of the inner involucral bracts mostly obtuse or rounded; peduncles with coarse, erect, yellowish-based hairs mostly 1.5-3.0 mm long; mature receptacular bracts purple or dark brown...lb. var. zamorensis p. 149

1a. ALDAMA DENTATA La Llave & Lexarza var. DENTATA.

Gymnopsis dentata (La Llave & Lexarza) DC. Prodr. 5:561.

1836. Type: VERACRUZ: Córdoba, "in inundatis
rivuli Hueneyapa [Hueyhueyapa], ad Sanctum-Josephum
del Corval [Corral] Mexic."

Gymnopsis schiedeana DC. Prodr. 5:561. Type: VERACRUZ:

"inter segetes ad margines dumetorum Jalappam [Jalapam]."

G. Schiede 225 (Holotype B; isotype MO!).

Sclerocarpus dentatus (La Llave & Lexarza) Benth. & Hook.

f., ex Hemsl. Biol. Cent. Am. Bot. 2:164. 1881.

Sclerocarpus schiedeanus (DC.) Benth. & Hook. f., ex

Hemsl. Biol. Cent. Am. Bot. 2:164. 1881.

Sclerocarpus kerberi Fourn. Bull. Bot. Soc. Fr. 20:183.

1883. Type: VERACRUZ: Córdoba, 31 Jul 1882.

E. Kerber 19 (Holotype M; isotype K!; type fragment F!).

Sclerocarpus coffeaecolus Klatt, Ann. Naturh. Hofmus.

Wein. 9:360. 1895. Syntypes: COLOMBIA [VENEZUELA]:

Valle de Aragua, Hacienda Palmar de San Matthes [Matheo],

E. Otto [811?] (Isosyntypes GH! K!; type fragment US!);

Moritz 25(56), no date or locality; Grosourdy, 1862,

without collection number or locality.

Sclerocarpus schiedeanus var. elongatus Greenm. Proc. Am.

Acad. 32:309. 1897. Syntypes: VERACRUZ: Wartenburg,

near Tantoyuca, 1895, L. C. Ervendberg 98, 99 (GH!);

MORELOS: fields around Cuernavaca, 31 Oct 1896, C. G.

Pringle 6606 (GH! MICH! MO! NY! US!).

Gymnolomia acuminata Blake ex Robinson, Proc. Am. Acad.

49:505. 1913. Type: TAMAULIPAS: "prope Gómez Farías,"
13-21 Apr 1907, E. Palmer 582 (Holotype GH!; isotypes
F! NY! US!).

Sclerocarpus elongatus (Greenm.) Greenm. & Thompson, Ann.
Mo. Bot. Gard. 1:412. 1915.

Pubescence of the younger portions of the stem, branches, and peduncles mostly strigose-pilose with white, appressed or spreading hairs mostly less than 1.5 mm long; receptacle mostly convex on the living plant, becoming hemispheric or subglobose after shedding of the achenes; inner involucral bracts mostly longer than the outer, the apex rarely broadly acute, mostly obtuse or rounded; exposed abaxial surface of the involucral bracts scabrous or strigose with mostly appressed hairs less than 1 mm long; ray achenes with a pappus of fused scales or irregular membranes to 0.3 mm high at the angles; mature marginal receptacular bracts mostly radially compressed, subtriangular in cross section, the surface light brown, stramineous or mottled, strongly wrinkled corrugate with prominent wing-like ribs laterally; marginal disk achenes with the pappus a low, often spreading, crown of basally-fused bristles; chromosome number, $n = 17$ (Feddema 1541, 1556, MICH).

Eastern Mexico, including southern Tamaulipas and Veracruz; central Mexico, including Querétaro, Mexico and Morelos; western Mexico, including Nayarit, Jalisco, Colima and Michoacan; southern Mexico, including Puebla, Oaxaca

and Chiapas; British Honduras, Honduras, Guatemala and Northern Venezuela.

Specimens examined:

MEXICO: TAMAULIPAS: 4 mi S of Jaumave, 7 Jul 1949, Stanford, Lauber & Taylor 2325 (NY, US); vicin. Gómez Farías, 13-21 Apr 1907, E. Palmer 582 (F, GH, TEX, US); 9 mi N of Aldama, 10 Dec 1959, M. C. Johnston (TEX); 1 mi N of Tampico-Mante highway on road to Lomas del Real, 15 Feb 1960, Johnston 5151 (TEX).

VERACRUZ: Palmar, 7 Sep 1936, L. H. MacDaniels 889 (F); Wartenberg, near Tantoyuca, 1895, L. C. Ervendberg 98, 99 (GH); Zacuapan [Zacualpan] Nov 1930, C. A. Purpus 15012 (GH), Jan 1929, Purpus 12012 (F, US); 10 mi SE of Poza Rica, 10 Mar 1961, R. King 4137 (F, NY, TEX, US); Ojapa, 30 Jun 1910, C. R. Orcutt 5156 (MO, US); 3 mi SE of Santa Rosa, 13 Jun 1960, R. Oliver 148 (TEX); Jalapa, Jan 1894, C. L. Smith 1741 (MICH, NY); fields about Jalapa, 16 May 1900, C. G. Pringle 8338 (F, GH, MICH, MO, NY, US); near Jalapa, Aug 1901, J. N. Rose 6110 (NY, US); near Jalapa, 24 May 1899, Pringle 7772 (MICH, US); Xalapa [Jalapa], T. Coulter 360 (K); Orizaba, 1855, F. Muller 778, 1584 (NY); Orizaba, 9 Aug 1924, G. L. Fisher 215 (US); Orizaba, 28 Jan 1894, E. W. Nelson 50b (US); Orizaba, 24 Apr 1938, E. K. Balls 4307 (US); Orizaba, 23 Jul 1891, H. E. Seaton 16 (F, GH, NY, US); 5 mi E of Orizaba, 26 Jan 1960, King 2352 (TEX); Fortín, Feb 1883, E. Kerber 272 (F, K, US); 9 km SW of Nogales, 5 Aug 1961, Feddema 1541 (MICH); Córdoba, 28 Jul 1935, G. L. Fisher 35337 (F, MO, NY, US); Córdoba,

8 Aug 1926, Fisher 125 (US); Córdoba, 6 Apr 1910, Orcutt 3432 (F); Córdoba, Aug 1938, E. Matuda 779 (MICH); near Córdoba, Jan 1906, J. M. Greenman 194 (F), 25 Jan 1906, Greenman 151 (GH); Valley of Córdoba, 23 Dec 1865, M. Borgeau 1623 (GH), 1626 (K, US); 14 mi E of Córdoba, 4 Feb 1959, D. Hunsacker II (TEX); 1 mi S of Cuitláhuac, 6 Jun 1960, King 2677 (MICH, NY, TEX, US); Motzorongo, 22 Feb - Mar 1894, Nelson 135 (US); near Omealca [Omealco], 6 Mar 1894, Nelson 175 (US); 14 mi SW of Veracruz, 27 Jan 1960, King 2406 (TEX, US); 6 mi N of San Andrés Tuxtla, 6 Aug 1961, Feddema 1568 (MICH).

QUERETARO: Querétaro, 23 Nov 1925, Juzepczuk 694, 695 (US); Querétaro, 1910-19-13, Bro. Agniel 10405 (F, GH, US).

MEXICO: Santo Tomás, 31 Aug 1952, Matuda 27497 (NY,US); Chorrera, Dist. Temascaltepec, 1 Sep 1932, G. B. Hinton 2041 (K, MO, NY, US); Limones, Dist. Temascaltepec, 11 Jul 1932, Hinton 2517 (K, MO, NY, US); Tempincla, Dist. Temascaltepec, 18 Apr 1932, Hinton 512 (K).

MORELOS: fields around Cuernavaca, 31 Oct 1896, Cuernavaca, 15 Nov 1865, M. Borgeau 1212 (K); Acapanzingo, 6 Dec 1925, Woronow & Juzepczuk 871 (US); Valley near Cuantla, 28 Oct 1900, Pringle 9061 (MICH, NY, US); 5 mi SE of Yautepec, 19 Jun 1960, King 2912 (MICH, NY, TEX, US).

GUERRERO: Pungarabato, Dist. Coyuca, 9 Jan 1934, Hinton 5441 (US); Taxco, 23 Dec 1936, R. Q. Abbott 184 (GH); environs of Taxco, 2 Jan 1936, Abbott 40 (GH).

MICHOACAN: Coalcomán, 13 Mar 1939, Hinton 13622 (GH, MO, NY, US); 2 km NW of Zitácuaro, 14 Aug 1961, Feddema 1666, 1698 (MICH).

COLIMA: Tuxpán Canyon, 3 Nov 1910, C. R. Orcutt 6536 (US).

JALISCO: Ocotlán, 25-31 Dec 1902, Nelson 6516 (GH, NY, US); Ocotlán, 1900, D. R. Furness (F); 8 mi SW of Pihuamo, 6 Dec 1950, McVaugh & Koelz 1527 (MICH); 3 km SE of Mezquitic, 4 Nov 1963, Feddema 2436 (MICH); approx. 15 km NW of Tepalcatepec, Michoacán, 26 Oct 1963, Feddema 2243 (MICH); Jaday, 6 Jul 1959, L. Davis (TEX).

NAYARIT: 4 mi W of Ixtlán del Río, 10 Aug 1960, King 3681 (MICH, NY, TEX, US); Tepic, 10 Aug 1960, King 3668 (TEX, US); Tepic, 5 Jan - 6 Feb 1892, Palmer 1860 (F, GH, MICH, NY, US).

PUEBLA: route 115, just S of Morelos-Puebla border, 19 Jun 1960, King 2919 (MICH, NY, TEX, US).

OAXACA: near Santo Domingo, 18 Jun 1895, Nelson 2705 (GH, US); S. of Etla, 1 Feb 1960, King 2509 (TEX, US); Valley of Oaxaca, 22 Nov 1894, Pringle 5680 (GH); Valley of Oaxaca, 14 Nov 1894, Lucius C. Smith 305 (GH); Oaxaca, Jul-Aug 1900, Conzatti & Gonzalez 995 (GH); 4 mi S of Oaxaca, 21 Jun 1960, King 2947 (MICH, NY, TEX, US); 9 mi NW of Oaxaca, 27 Jul 1960, King 3516 (MICH, NY, TEX, US).

CHIAPAS: 33 mi S of Tuxtla Gutiérrez, 27 Jun 1960, King 3103 (MICH, NY, TEX, US).

HONDURAS: around Copán, 9 Jan 1907, H. Pittier 1838a (F, US).

BRITISH HONDURAS: pine ridge near Manatee lagoon,
M. E. Peck 26 (GH).

GUATEMALA: Dept. Sololá, Lago de Antlán, near Panajachel,
 5 Jul 1960, King 3243 (F, GH, TEX, US); Dept. Izabal,
 Gulán [Gualán], 26 May 1919, S. F. Blake 7682 (US); vicin.
 Zacapa, 7-16 Oct 1940, P. C. Standley 74672 (F); vicin.
 Jalapa, 7-18 Nov 1940, Standley 76455 (F); vicin. Jutiapa,
 24 Oct - 5 Nov 1940, Standley 75100 (F); near Ipala, Dept.
 Chiquimula, 23 Oct 1939, J. A. Steyermark 30297 (F);
 Valley of Río Chiquimula, Dept. Chiquimula, 21 Oct 1939,
Steyermark 30175 (F); below Cerro Redondo, Laguna Los
 Pinos, Dept. Santa Rosa, 25 Oct 1942, Steyermark 52165 (F);
 Río Pimila, Apr 1892, Heyde & Lux 3419 (F, GH, US); Agua
 Blanca, Nov 1913, R. Tejada 99 (US).

VENEZUELA: Caracas, 16 Mar 1899, A. H. Moore 27 (GH);
 Caracas & vicin., 16 Dec 1920, L. H. & E. Z. Bailey 208
 (NY, US); near Caracas, between Cotiza and Los Venados,
 Oct 1924, A. Allart 65 (US); "prope coloniam Tovar" 1854-
 1855, Fendler 685 (GH, K, MO); Lower Cotiza, near Caracas,
 21-27 Jul 1917, H. Pittier 7288, 7311 (GH, US); between
 Caracas and Guaira, 17 Oct 1916, J. N. Rose 21656 (US);
 Federal Dist., old road from Caracas to La Guayra [Guaira],
 28 Feb 1913, Pittier 5908 (NY, US); La Florida, near
 Caracas, 12 Oct 1938, A. H. G. Alston 5454 (NY, US); State
 of Miranda, S of Los Teques, 10 Dec 1943, Steyermark 54979
 (F, NY, US); Miranda, between Las Canales and El Encanto,
 Nov 1942, T. Lasser 687 (US); Losa, Federal Dist., May 1938,
F. T. Tamayo 208 (US); alrededor de San Juan de Los Moros,

Guarico, 29 Nov 1938, Llewelyn Williams 10876 (A, F, US);
Ingomar, Sept 1935, Pittier 13587 (MO, US).

1b. ALDAMA DENTATA La Llave & Lexarza var. ZAMORENSIS

Feddesia, var. nov. hirsuta, pilis plerumque 1-3 mm longis; involucris bracteae interiore anguste acutae vel forte acuminatae; receptaculum plerumque ovatum; marginis disci paleae maturae purpureae, laevigatae, vel leviter aspero-corrugatae; radiorum achaenia epapposa vel pappus vix 0.1 mm longus.

Pubescence of the younger portions of the stem, branches and peduncles mostly hirsute with stiff, erect hairs 1.5-3.0 mm long with prominent, yellowish bases; receptacle low-convex or ovoid-conoid when living, becoming strongly ovoid-conoid after the fall of the achenes; inner involucre bracts only slightly longer than the outer, the apex narrowly acute or strongly acuminate; exposed adaxial surface of the involucre bracts with mostly suberect, yellowish hairs mostly more than 1.4 mm long, sometimes to 2.8 mm long; ray achenes epappose or with a pappus only suggested by low irregularities on the apical margin; mature marginal receptacular bracts mostly laterally compressed or somewhat radially compressed, the surface mostly slightly irregularly wrinkled, mostly without prominent, wing-like ribs laterally; marginal disk achenes epappose or with the pappus reduced to a low collar or irregular rim; chromosome number $n = 17$ (*Feddesia* 1724 MICH).

Western Michoacán and southeastern Jalisco, at elevations of 1500 to 1800 m, flowering July to September.

Type: MICHOACAN: 27 km SE of Zamora, 16 Aug 1961,
Feddema 1724 (Holotype MICH!).

Specimens examined:

JALISCO: 1 mi W of Ayo el Chico, 23 Aug 1958, R. McVaugh
17208 (MICH).

MICHOACAN: 2 mi E of Zamora, 6 Aug 1960, R. King 3645
(MICH, NY, TEX, US).

EXCLUDED SPECIES

1. ALDAMA MONTANOA Schultz Bip. ex K. Koch, Wochenschr.
Gartn. 7:406. 1846.
Montanoa frutescens (Mair.) Hemsl. Biol. Centr. Bot.
2:165. 1885.

SUMMARY

The generic name Sclerocarpus was first published by J. N. Jacquin (1781) in a volume of colored plates of rare plants, one of which bore the title Sclerocarpus africanus. The genus Aldama and the species Aldama dentata were described by La Llave & Lexarza (1824) from a plant collected in Veracruz. Both of these plants resembled Helianthus but were peculiar in that the receptacular bracts completely and closely enclosed the achenes and were somewhat thickened and ornamented. DeCandolle (1836) recognized Sclerocarpus Jacquin but combined Aldama with Gymnolomia H. B. K., renaming the combined genus Gymnopsis. DeCandolle believed that the plants which had previously been assigned to Aldama dentata, really represented two different species which he recognized in his new genus. For some time after DeCandolle, plants with the peculiar receptacular bracts were assigned to Gymnopsis. Later, however, Aldama was again considered the proper genus for most of these plants, but for the past century all have been assigned to Sclerocarpus.

The name Aldama has priority over Gymnopsis as applying to the plant of La Llave and Lexarza and Aldama is separable from Sclerocarpus on the basis of many morphological characters of the flowers, achenes and receptacular bracts as well as their chromosome numbers; thus both genera must be maintained as distinct entities. On the basis of morphology and chromosome numbers, the species of Sclerocarpus can be placed in four groups in which the

haploid chromosome numbers are 11, 12, 14, and 18 respectively. Aldama has one species which has two varieties, both with a chromosome number of 17.

Both genera, with the exception of a single species of Sclerocarpus are distributed in tropical America from Texas to northern South America with concentrations from Mexico to Costa Rica. Sclerocarpus africanus is unique with a distribution which is mainly African with a disjunct population in India and West Pakistan and presumably adventive populations in northern South America and the American Virgin Islands. Sclerocarpus has endemic species in western Mexico and one localized in eastern Guatemala and western Honduras, and two rather widespread species. One of the latter, Sclerocarpus divaricatus, which ranges through most of Mexico to Costa Rica, is slightly differentiated into western and eastern populations in Mexico. Sclerocarpus uniserialis has one of its varieties with two color forms restricted to southeastern Texas, another which ranges from Tamaulipas to Chiapas, and a third essentially restricted to Guerrero. The last two varieties give evidence of hybridization and introgression in southern Mexico, and all varieties have been crossed in the laboratory. There is slight evidence for some hybridization between Sclerocarpus divaricatus and Sclerocarpus multifidus in Michoacan. Aldama dentata is distributed from Mexico to Honduras probably with adventive populations in northern South America. One variety is spread over the

entire range of the species, and another is endemic in the region east of Lake Chapala in Mexico.

Both genera are somewhat weedy in habit and neither has much economic importance other than the occasional use as forage. Their distribution and evolution was probably influenced by man and agriculture. Both genera probably originated from a common primitive Helianthoid ancestor, and although modern Sclerocarpus is not closely related to Aldama or any other genus, Aldama is rather closely related to Viguiera from which it may have been derived.

Sclerocarpus could have been derived from a primitive ancestor with a haploid chromosome number of six which by polyploidy gave rise to intermediate forms with a haploid number of twelve, which in turn gave rise to the modern species groups mostly by aneuploidy. These hypothetical intermediate ancestors are probably not closely related to any modern species.

BIBLIOGRAPHY

- Abrams, L. and Ferris, R. S. 1960. Illustrated flora of the Pacific States. Vol. 4. pp. 169-171. Stanford University Press. Stanford.
- Benson, L. 1962. Plant Taxonomy, Methods and Principles. p. 415. Ronald Press Co. New York.
- Bentham, G. 1845. in Hines, R. B., ed. Botany of the voyage of H.M.S. Sulphur, 1836-42. Smith Elder & Co. London.
- Bentham, G. and Hooker, J. D. 1873. Genera plantarum. Vol. 2. pp. 189-199. Reeve & Co. London.
- _____. 1881. in Hemsley, W. B., Biologia Centrali-Americana. Botany. Vol. 2. p. 164. R. H. Porter. London.
- Blake, S. F. 1913. A revision of Encelia and some related genera. Contr. Gray Herb. 41:346-396.
- _____. 1917. New and noteworthy Compositae, chiefly Mexican. Contr. Gray Herb. 52:16-59.
- _____. 1918. A revision of the genus Viguiera. Contr. Gray Herb. 54:1-205.
- _____. 1921. Revisions of the genera Acanthospermum, Flourensia, Oyedaea, and Tithonia. Contr. U.S. Nat. Herb. 20:383-436.
- _____. 1922. New plants from Guatemala and Honduras. Contr. U.S. Nat. Herb. 24:1-32.
- _____. 1930. Notes on certain type specimens of American Asteraceae in European herbaria. Contr. U.S. Nat. Herb. 26:227-263.

- Blake, S. F. 1945. Asteraceae described from Mexico and the southwestern United States by M. E. Jones, 1908-1935. *Contr. U.S. Nat. Herb.* 29:117-137.
- Candolle, A. P. de, 1836. *Prodromus systematis naturalis regni vegetabilis*. Vol. 5. pp. 1-107. Paris.
- Carlquist, S. 1961. *Comparative plant anatomy*. Holt, Rinehart and Winston. New York.
- Cassini, H. 1822. in *Dictionnaire science naturelles etc.* Vol. 25. F. G. Levrault, Strasbourg: Le Normant, Paris.
- Cronquist, A. J. 1955. Phylogeny and taxonomy of the Compositae. *Amer. Midl. Nat.* 5:478-511.
- Eggers, Baron H. F. A. 1879. *Flora of St. Croix and the Virgin Islands, West Indies*. Bulletin of the U.S. National Museum. No. 13. 133 pp. Washington.
- Fournier, E. 1833. *Plantae Mexicanae a Edm. Kerbero collectae*. *Bull. Bot. Soc. Fr.* 30:181-188.
- Gray, A. 1850. *Plantae Lindheimerianae*. *Journ. Boston Soc. Nat. Hist.* 6:228.
- _____. 1873. Determinations of a collection of plants made in Oregon by Elihu Hall during the summer of 1871, with characters of some new species and various notes. *Proc. Am. Acad.* 8:372-412.
- Greenman, J. L. 1897. Descriptions of new and little known plants from Mexico. *Proc. Am. Acad.* 32:295-301.
- _____. 1904. Diagnoses and synonymy of Mexican and Central American spermatophytes. *Proc. Am. Acad.* 40:28-52.

- Greenman, J. L. 1912. Diagnoses of new species and notes on other spermatophytes, chiefly from Mexico and Central America. Field Mus. Publ. Bot. 2:329-350.
- Greenman, J. L. and Thompson, C. H. 1914. Diagnoses of flowering plants, chiefly from the southwestern United States and Mexico. Ann. Missouri Bot. Gard. 1:405-413.
- Heiser, C. B. Jr. 1963. Artificial intergeneric hybrids of Helianthus and Viguiera. Madroño 17:118-127.
- Hoffmann, O. 1894. Compositae in Engler and Prantl, Natürlichen Pflanzenfamilien. 4, pt. 5:87-375.
- Hooker, W. J. 1837. Icones plantarum. Vol. 2. t. 145 and facing page. Longman, Rees, Orme, Brown, Greene & Longman. London.
- Jacquin, J. N. 1781. Icones Plantarum rariorum. Vol. 1. p. 17. t. 176. Christianum Fredericum Wappler. Vindobonae.
- _____. 1787. Tria genera plantarum nova, ex Horto Botanico Viennensi. Nova Acta Helvetica 1:36-38.
- Jones, M. E. 1933. New species and notes. Contr. West. Bot. 18:20-85.
- Keck, D. D. 1940. The identity of Madia dissitiflora (Nutt.) Torr. & Gray. Madroño 5:169-170.
- Klatt, F. W. 1895. Neue Compositen aus dem Wiener Herbarium. Ann. Naturh. Hofmus. Wien. 9:355-368.
- La Llave, P. and Lexarza, J. 1824. Novorum vegetabilium descriptiones in lucem prodeunt. p. 14. M. Rivera. Mexico.

- Lanjouw, J. and Stafleu, F. A. 1964. Index herbariorum.
Part 1. The herbaria of the world. ed. 5.
International Bureau for Plant Taxonomy. Utrecht.
- Lessing, F. C. 1830. De synanthereis Herbarii Regii
Berolinensis. Dissertatio secunda. Nassauviae.
Linnaea 5:1-236.
- _____. 1834. De plantis Mexicanis a G. Schiede M. Dre.
collectis nuntiam adfert D. F. Schlechtendal.
(continued) Linnaea 9:262-272.
- Linnaeus, C. 1753. Species plantarum. Vol. 2. pp. 904-906.
Holmiae.
- Munz, P. A. 1959. A California flora. University of
California Press. Berkeley.
- Murray, A. 1784. Systema vegetabilium. Ed. 14. p. 783.
C. Dieterich. Göttingen.
- Rose, J. N. 1891. List of plants collected by Dr. Edward
Palmer in western Mexico and Arizona in 1890. Contr.
Nat. Herb. 1:91-116.
- Rusby, H. H. and Blake, S. F. 1924. in Blake. New
American Asteraceae. Contr. U.S. Nat. Herb. 22:587-661.
- Smith, Sir Edward. 1815. "Sclerocarpus". in Rees, A.
Cyclopaedia. Vol. 33. Longman, Hurst, Rees, Orme, &
Brown. London.
- Small, J. K. 1913. Flora of the southeastern United
States. ed. 2. Published by the author. New York.
- Small, James. 1919. The origin and development of the
Compositae. William Wesley & Son. London.

- Solbrig, O. T. 1963. The tribes of the Compositae in the southeastern United States. *Journ. Arnold Arb.* 44:436-461.
- Standley, P. C. 1938. *Flora of Costa Rica*. Field Mus. Publ. Bot. 18:783-1616.
- Stearn, W. T. 1961. Botanical gardens and botanical literature in the eighteenth century. in Stevenson, A., compiler. *Catalogue of botanical books in the collection of Rachel McMasters Miller Hunt*, Vol. 1, Part 2. Hunt Botanical Library. Pittsburgh.
- Torrey, J. and Gray, A. 1842. *Flora of North America*. Vol. 2. pp. 316-317. Wiley and Putnam. New York.
- Turner, B. L. 1960. Documented chromosome numbers of plants. *Madroño*. 15:221.
- Turner, B. L., Powell, M., and King, R. M. 1962. Chromosome numbers in the Compositae. VI. Additional Mexican and Guatemalan species. *Rhodora* 64:251-271.
- Vatke, W. 1875. *Plantae Abyssinicae collectionis Nuperrimae (a. 1863-8). Schimperianae enumeratae*. *Linnaea* 39:475-518.