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A Biosystematic Study of *Heterotheca* section *Pityopsis*

Frank D. Bowers
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To the Graduate Council:

I am submitting herewith a dissertation written by Frank D. Bowers entitled "A Biosystematic Study of *Heterotheca* section *Pityopsis*." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Botany.

A. Murray Evans, Major Professor

We have read this dissertation and recommend its acceptance:

Frank W. Woods, A. J. Sharp, H. R. DeSelm

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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November 14, 1972

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Accepted for the Council:

Hilton A. Smith
Vice Chancellor for
Graduate Studies and Research

A BIOSYSTEMATIC STUDY OF *HETEROTHECA* SECTION *PITYOPSIS*

A Dissertation

Presented to

the Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

---

by

Frank D. Bowers

December 1972

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ABSTRACT

A biosystematic study of the section Pityopsis of the genus Heterotheca was undertaken. Cytological, morphological, chromatographic, and hybridization studies were utilized to provide a basis for taxonomic treatment of the taxa. The species were divided into two broad groups; the Heterotheca graminifolia group (H. adenolepis, H. aspera, H. graminifolia, H. microcephala var. microcephala and var. aequilifolia, and H. oligantha) and the H. pinifolia group (H. falcata, H. flexuosa, H. pinifolia, and H. ruthii). Heterotheca ruthii appears to be intermediate between the two groups and is closely related to H. oligantha.

Cytology indicates the diploid species (N=9) are prominent with only H. adenolepis (both diploids and tetraploid), H. graminifolia, and H. oligantha being tetraploids (N=18). Pollen measurements were obtained showing tetraploids being significantly larger (except for H. adenolepis).

Paper chromatographs were somewhat inconclusive but generally followed the other taxonomic evidence for the section.

It is thought that H. graminifolia was derived via autopolyploidy from H. microcephala. Heterotheca adenolepis

is thought to have been derived from an allopolyploid hybrid between H. aspera and H. microcephala. Heterotheca oligantha has a limited range in Florida and Alabama but appears closely related to H. graminifolia and H. ruthii. Heterotheca pinifolia, H. falcata, H. flexuosa, and H. ruthii apparently were derived from one or more primitive ancestors which migrated from an Appalachian center of origin to the Coastal Plain, became geographically separated and evolved into the four entities listed above. Heterotheca ruthii appears to be the most primitive of the four species. All are limited in range with H. ruthii found only in the Hiwassee Gorge of East Tennessee; H. flexuosa in a few counties in Florida; H. pinifolia in a few counties in the Sand Hills of Georgia and North and South Carolina, and H. falcata in sand areas in five northeastern states. These four species have relatively few genetic barriers but are widely separated geographically.

TABLE OF CONTENTS

CHAPTER		PAGE
I.	INTRODUCTION	1
II.	NOMENCLATURAL REVIEW	4
	The Merger of *Heterotheca* and *Chrysopsis*	7
	Reported Chromosome Numbers	9
III.	METHODS AND MATERIALS	12
IV.	RESULTS	19
	General Morphology	19
	Cytological Variation	23
	Chemotaxonomic Studies	23
	Breeding System	47
	Hybridization Experiments	48
	General Ecology	55
V.	PHYLOGENETIC CONSIDERATIONS	58
VI.	TAXONOMIC TREATMENT	79
	Generic Treatment	79
	Key to the Sections of *Heterotheca*	82
	Sectional Treatment	83
	Key to the Species of Section *Pityopsis*	89
	Species Treatment	92
VII.	SUMMARY	175
LITERATURE CITED		178
APPENDIX		185

CHAPTER PAGE

Appendix A 186

VITA 188

LIST OF TABLES

TABLE PAGE

I. Reported Chromosome Numbers for *Heterotheca* (Also *Chrysopsis*) 10

II. The Number of Specimens of Section *Pityopsis* Studied in Detail 13

III. Chromosome Numbers in *Heterotheca* Sect. *Pityopsis* 24

IV. Pollen Size and Stainability. 28

V. Populations of *Heterotheca* Examined for Flavonoids by Paper Chromatography. 35

VI. Chromatographic Properties of Compounds of *Heterotheca* Section *Pityopsis* and Selected Other Species of Sections *Chrysopsis* and *Heterotheca* 38

VII. Chromatographic Paired Affinity Values of *Heterotheca* Taxa. 46

VIII. Data on Habitat Observations as Noted on Herbarium Labels of Section *Pityopsis* (As Percentages). 56

IX. Characters and Character States Used in Section *Pityopsis* 60

X. Character States for the Taxa of Section *Pityopsis* 61

TABLE PAGE

XI. Computed Differences Between the Taxa in Section Pityopsis 63

XII. Differences Between Heterotheca adenolepis, H. aspera, and H. microcephala Var. microcephala. 97

XIII. Differences Between Heterotheca adenolepis, H. graminifolia, and H. microcephala Var. microcephala. 106

LIST OF FIGURES

FIGURE PAGE

1. Traced Drawings from Photographs of Chromosomes of *Heterotheca* Species. 26
2. Pollen Sizes of *Heterotheca* Section *Pityopsis* Showing Mean Size, Standard Deviation, and Range 33
3. A Composite Chromatogram of Species of *Heterotheca* 36
4. Chromatographic Profiles of *Heterotheca* Species (Including Species in Section *Chrysopsis* and *Heterotheca*). 40
5. Chromatographic Profiles of *Heterotheca* Species (*Heterotheca graminifolia* Group). 42
6. Chromatographic Profiles of *Heterotheca* Species (*Heterotheca pinifolia* Group) 44
7. Artificial Crosses in *Heterotheca* Section *Pityopsis* 50
8. Modified Wagner Tree of *Heterotheca* Section *Pityopsis* 64
9. Paired Affinity Indices of Species in *Heterotheca* Section *Pityopsis* 65
10. Phylogeny Chart of *Heterotheca* Section *Pityopsis*. 68

FIGURE PAGE

11. Distribution Map of Section Pityopsis (Dotted Area) and Physiographic Province Map. 71

12. Distributions of Heterotheca Sections Ammodia, Chrysopsis, and Heterotheca 85

13. Type Specimen of Heterotheca aspera (Shuttlew.) Shinners. 95

14. Distribution of Heterotheca adenolepis and H. aspera. 98

15. Type Specimen of Heterotheca adenolepis (Fern.) Ahles 102

16. Type Specimen of Heterotheca microcephala Var. microcephala (Small) Shinners 116

17. Distribution of Heterotheca microcephala (Both Varieties). 118

18. Type Specimen of Heterotheca microcephala Var. aequilifolia Var. Nov.. 125

19. Isotype of Heterotheca graminifolia (Michx.) Shinners. 132

20. Type Specimen of Heterotheca graminifolia Var. latifolia Fern.. 134

21. Distribution of Heterotheca graminifolia and H. oligantha. 137

22. Type Specimen of Heterotheca ruthii (Small) Harms 149

FIGURE PAGE

23. Distribution of Heterotheca falcata, H. flexuosa, H. pinifolia, and H. ruthii 151

24. Lectotype of Heterotheca oligantha (Chapm.) Harms 154

25. Representative Specimen of Heterotheca falcata (Pursh) Harms 161

26. Type Specimen of Heterotheca flexuosa (Nash) Harms 166

27. Representative Specimens of Heterotheca pinifolia (Ell.) Ahles. 170

28. Population Sample Analysis of a Hybrid Swarm Between Heterotheca adenolepis (N=9) and Heterotheca pinifolia (N=9) Located in Moore County, North Carolina. 172

CHAPTER I

INTRODUCTION

Heterotheca (including Chrysopsis) is a temperate North American genus of the Compositae included in the yellow-flowered group of the Astereae. When Shinners (1951) submerged Chrysopsis into Heterotheca, he greatly increased the number of species in the latter, and his treatment is accepted as explained below. The closest relatives in the tribe Astereae have been thought to be Bradburia and Haplopappus (Harms, 1963), but no thorough work has been done to demonstrate this relationship. Gray (1884) treated both Heterotheca and Chrysopsis as separate taxa but included all known species at that time. Chrysopsis was discussed by Greene (1894) in its entirety; however, by then, some western taxa were yet unknown.

The four sections included under Heterotheca are Ammodia, Chrysopsis, Heterotheca, and Pityopsis. The discoid flowered species of section Ammodia were last treated taxonomically in Greene's (1894) paper, but later Munz (1959) and Keck (1960) mentioned them. Dress's (1953) monograph on the southeastern species of section Chrysopsis (including H. mariana, H. gossypina, and others) was never published in its entirety. The western taxa, including the

H. villosa complex of section Chrysopsis, were treated by Harms (1963). Wagenknecht (1960) monographed section Heterotheca before its merger with Chrysopsis.

Section Pityopsis is a distinct group within Heterotheca with mostly sericeous-pubescent herbage, fusiform or cylindric achenes, and parallel-veined, graminiform to linear leaves. Small (1933) gave generic distinction to Pityopsis, but which proved unacceptable to later botanists. Fernald (1942) described Pityopsis as a "hardly worthwhile genus."

The latest publications relating to this section have been by Small (1933), Fernald (1942) in which he studied the H. graminifolia complex in Virginia and the Carolinas, and Harms (1969). Dress (1953), in an unpublished Ph.D. dissertation, studied the group and followed Small (1933) except in the H. graminifolia complex which he regarded as a single species with four varieties.

Harms' (1969) paper was a preliminary conspectus in which he solved some of the nomenclatural problems by using a conservative taxonomic viewpoint. He indicated the paper was a

> . . . preliminary treatment to bring together the taxonomic and nomenclatural information on the group, provide a key to included species, serve as a vehicle for needed nomenclatural changes, and point up existing taxonomic problems needing further investigation.

The section Pityopsis has been difficult taxonomically

because of the distinct forms which appear in certain geographic regions and which appear to intergrade in others. Local floras are not adequate for the complex as a whole since the usually local collections contain only parts of wider geographic-taxonomic variation.

What has been needed in the Heterotheca section Pityopsis group is a biosystematic approach with the use of cytological, morphological, and ecological data to provide a clearer understanding of the inter-relationships. This should provide a basic framework for the interpretation of the taxonomy. This study has endeavored to provide the above data and interpretation through field work, the study of herbarium specimens, use of transplants for hybrid and variability studies, and laboratory studies.

CHAPTER II

NOMENCLATURAL REVIEW

Ignoring earlier polynomials, the first valid binomial publication of a species now considered in this genus (Heterotheca) was Inula mariana by Linnaeus (1763). There is a specimen in his collections of this plant collected by Kalm in 1754 (Savage, 1945). Later workers, following the lead of Linnaeus, have described other species of Inula from North America. Some, however, did not follow him. Thomas Walter in 1788 described, in his Flora Caroliniana, Erigeron pilosum (= Heterotheca gossypina), Willdenow (1803) described a new species Erigeron nervosum (= Heterotheca graminifolia) and Poiret (1808) published another Erigeron, E. glandulosum (= Heterotheca microcephala).

In Fraser's Catalogue, Nuttall (1813) named Sideranthus integrifolius (= Heterotheca villosa), now a nomen nudum. Later, Pursh (1814) named Amellus villosus (= Heterotheca villosa) and reduced Sideranthus integrifolius in synonymy with it. While Sideranthus was the first new generic name for any species of Heterotheca, the description in Fraser's Catalogue is deemed inadequate by most authors (Harms, 1963).

Cassini (1817) provided the name Heterotheca based upon Inula subaxillares but didn't transfer it officially until 1821. At that time, he also described Heterotheca lamarckii and later in 1827, Heterotheca inuloides. He aos named a new genus Diplopappus (Cassini, 1817) to receive the double-pappus species of Aster and Inula but failed to typify it with a species until 1819 (D. lanatus = Heterotheca gossypina).

Rafinesque (1818) endeavored to separate from Inula the double-pappus plants under the name Diplogon. However, he made no new combinations, stating merely that "Inula mariana with some other species must form the genus Diplogon, Ref. N. G." Later Kuntz (1891) tried to revive Diplogon to supplant Chrysopsis but was opposed by Greene (1894) and Rydberg (1895).

Chrysopsis was described as a section under Inula by Nuttall (1818) to include species of North America in Inula and Aster which had double pappus, anthers naked at the base, and mostly yellow flowers.

Chrysopsis was raised to the rank of genus by Elliott (1829) who included most of Nuttall's listed species except the non-yellow members. He added also C. divaricata (= Haplopappus divericata). Chrysopsis (Nutt.) Ell. was conserved over Diplogon Raf. in the list of "Nomina Generica Conservanda" published in the International Code of

Botanical Nomenclatural (1952).

Other monotypic genera reduced to synonymy include the genus Diplocoma (D. villosa) which was described by Don (1828) and is a synonym of Heterotheca as a result of D. villosa being conspecific with H. subaxillaris (Wagenknecht, 1960).

Hectorea villosissima De Candolle (1836) is Heterotheca villosa (Harms, 1963). Schulz (1853) described Heyfeldera sericea but which was listed as a synonym for H. graminifolia by Bentham and Hooker (1873).

Nuttall in 1841 published the new genus Ammodia based on A. oregona. This later was reduced by Gray (1884) to a section under Chrysopsis.

Nuttall (1841) also established the new genus Pityopsis deriving its species from Chrysopsis because of their "grass-like leaves . . . naked or . . . very long flaky, silk-like, more or less deciduous pubescence . . ." He also mentions the shape of the achene which differs from that in section Chrysopsis. Pityopsis pinifolia (Ell.) Nuttall became the type species for the new genus. Torrey and Gray (1843) reduced Pityopsis to a section under Chrysopsis. Although most later authors have rejected Pityopsis as a genus, Small (1933) decided to place it in his manual as a genus distinct from Chrysopsis.

The Merger of Heterotheca and Chrysopsis

The separation of Heterotheca and Chrysopsis has been based upon the epappose ray florets found in Heterotheca. Shinners (1951) placed Chrysopsis under the older name Heterotheca mainly because the Mexican Heterotheca chrysopsidis has been found with occasional vestigial pappus in the ray florets and also because section Ammodia (of Chrysopsis) has rayless flowers with outer pappus reduced or vestigial. Before this, Baillon (1886) placed these genera along with eight other yellow-flowered genera together in a single genus Hystenonica, but later botanists did not follow him.

The study of Wagenknecht (1960) supported the merger by Shinners because he found approximately 3 percent of the plants in Heterotheca studied by him had a rudimentary pappus. He also found a specimen from San Patricio County, Texas, that had fully developed ray floret pappus like the disc flowers. Harms (1963) also supported the merger as did Wagenknecht. Harms found double pappus on ray florets of H. chrysopsidis from Mexico and found seedling morphology similar between H. subaxillaris and the H. (Chrysopsis) villosa complex while H. pilosa and H. mariana (both members of Chrysopsis) were easily distinguished. Harms (1965) produced "intergeneric" crosses between Heterotheca latifolia var. macgregoris and H. (Chrysopsis) berlandieri

having an average pollen stainability of 21 percent, almost normal pairing of the chromosomes at diakensis and metaphase I, normal disjunction at anaphase I which indicate little chromosomal differences. This indicates at least in this instance the generic relationship between Heterotheca and Chrysopsis is close and should constitute strong evidence for the merger of the two genera.

There is much further study to be done in this area in attempting additional crosses between the four sections in Heterotheca. The sections Ammodia and Heterotheca appear to be taxa derived from or closely related to Heterotheca (Chrysopsis) villosa (Harms, 1969). Harms (1963) in his Ph.D. dissertation first divided section Chrysopsis into two sections [Chrysopsis and Hirsuticaulis (Harms)] in which he placed the annual and biennial and low chromosome (N=4, 5) species in section Chrysopsis and the others (perennial and N=9, 18) in a new section Hirsuticaulis Harms. A later publication (Harms, 1968) indicated that he felt the sections should be reunited under Chrysopsis. Section Chrysopsis, while studied by Dress (1953) and Harms (1963), still needs further work in order for the species to be easily distinguished, especially in Florida and in the western United States. Pityopsis, while a distinct group, certainly belongs in Heterotheca, but further study is needed.

Even though it has necessitated a number of transfers

from Chrysopsis to Heterotheca, Shinners (1951) has been followed in the merger and at present the genus Heterotheca should be separated into four distinguishable sections: Ammodia, Chrysopsis, Heterotheca, and Pityopsis.

Reported Chromosome Numbers

Chromosome numbers recorded for species of Heterotheca are shown in Table I. As in many Astereae, the basic number is 9 with tetraploids in sections Chrysopsis and Pityopsis. Reduction must have occurred in section Chrysopsis within the annual and biennial species (N=4, 5). Turner (1961) believed that the N=4 and N=5 were the basic numbers of the section, but later workers have disagreed with this view. Harms (1963) and Jackson (1962) indicated that the total length of the chromosome of Heterotheca pilosa (N=4) was only slightly less than that found in H berlandieri (N=9) and thus Harms contended that aneuploidy is a better explanation than polyploidy.

TABLE I

REPORTED CHROMOSOME NUMBERS FOR *HETEROTHECA* (ALSO *CHRYSOPSIS*)

Entity	Location	N	Author
Sect. *Ammodia*			
martirensis	Mexico (Baja)	9	Moran (1969)
Sect. *Chrysopsis*			
bolanderi	California	9	Raven, Solbrig, Kyhos, and Snot (1960)
foliosa	New Mexico	18	Jackson (1959)
pilosa	Texas	5	Turner (1959) (in error)
	Texas	4	Cherry (1959)
camporum	Missouri and Tennessee	18	Harms (1963)
canescens	Kansas, Oklahoma, Texas	9	Harms (1963)
horrida	Arizona, Colorado, New Mexico	9	Harms (1963)
stenophyla	South Dakota, Kansas, Oklahoma	18	Harms (1963)
	Oklahoma, New Mexico, Texas, Kansas	9	Harms (1963)
villosa	Colorado, Kansas, Nebraska, New Mexico, Oklahoma, South Dakota, Texas, Wyoming	18	Harms (1963)
villosa var. *fastigrata*	California	9	Raven, Solbrig, Kyhos, and Snot (1960)

TABLE I (continued)

Entity	Location	N	Author
villosa var. *hispida*	Colorado	9	Raven, Solbrig, Kyhos, and Snot (1960)
villosa	Durango (Mexico)	9	Turner, Powell, and King (1962)
Sect. *Heterotheca*			
grandiflora	California	9	Heiser and Whitaker (1948)
	California	9	Raven, Solbrig, Kyhos, and Snot (1960)
inuloides	Mexico	9	Turner and Johnston (1961)
	Mexico	9	Turner, Ellison, and King (1961)
latifolia var. *latifolia*	Texas	9	Turner (1959)
latifolia var. *macgregoris*	Kansas	9	Jackson in Wagenknecht (1960)
Sect. *Pityopsis*			
graminifolia (= *microcephala*)	Florida	9	Turner, Ellison, and King (1961)
aspera (= *adenolepis*)	Mississippi	9	Jones (1965)
aspera (= *adenolepis*)	Alabama	18	Smith (1965)

CHAPTER III

METHODS AND MATERIALS

The following studies were done at The University of Tennessee (Knoxville) from 1969 to the present. Included in this study were the following techniques: field observations, collection of specimens for mass samples analysis (over 600), growing transplants and seedlings in a uniform greenhouse environment, pollen and chromosome analysis, chromatographic analysis, hybridizations attempts, artificial and natural hybrid analysis, and the study of 3,500 herbarium specimens from various herbaria (number of specimens studied in detail, Table II).

Collecting trips were made to New Jersey, Virginia, North and South Carolina, Georgia, Alabama, Florida, Mississippi, Louisiana, Arkansas, and Tennessee since 1969 to collect specimens of all the species for the techniques applied above. Other regions not visited were generally represented in the herbarium specimens.

The mass sample collections were made in a number of collection sites to sample variation within populations and species. The collections varied from 15 specimens or more depending upon the number of plants at the individual site. All species were collected in the field. These were collected as randomly as possible by selecting a specimen

TABLE II

THE NUMBER OF SPECIMENS OF SECTION *PITYOPSIS* STUDIED IN DETAIL

Taxa	Total Specimens Available (Herbarium and Field Collections)	Approximate Percentage Studied in Detail
Heterotheca adenolepis	765	10
Heterotheca aspera	70	80
Heterotheca falcata	414	10
Heterotheca flexuosa	109	50
Heterotheca graminifolia	950	10
Heterotheca microcephala var. *microcephala*	825	10
Heterotheca microcephala var. *aequilifolia*	98	50
Heterotheca oligantha	210	20
Heterotheca pinifolia	100	50
Heterotheca ruthii	59	85

every three to five steps depending on population size. Bizarre or unusual plants, if seen, were collected. Specimens were examined using a data sheet (see Appendix) with about 40 objective judgments. Collections of the author varied with species ranging from 36 to over 150 specimens per species. The greenhouse plants were equally divided between transplants and seedlings. Transplants were generally over 50 percent successful in surviving the shock of transplanting. Seedlings were quite successful when mature seeds were available for germination. The greenhouse provided a generally uniform environment for these plants. A select group of species (two plants each of Heterotheca graminifolia, H. oligantha, H. falcata, H. microcephala, and H. pinifolia) were also placed under long day conditions to study the effect on morphology and flowering. The greenhouse plants provided the specimens for crossing experiments.

Pollen analysis was obtained almost wholly from recent dried specimens stained with cotton blue in lactophenol for 24-48 hours (Harms, 1963). The dark blue stained grains were considered viable, and non- or lightly-stained or badly misshapen grains were considered non-viable (Hauser and Morrison, 1964). The percentage counts were based on 300 randomly selected grains. The pollen was obtained from one to two flowers from five different heads on a plant.

The measurements were taken of the pollen grain--one of the inside diameter of the pollen wall and the other of the largest exterior diameter including ornamentation. This was done at 1000X with a screw type ocular micrometer based upon 10 randomly selected grains obtained as in the pollen analysis above.

A modified Carnoy's solution (6:3:1 ethyl alcohol, chloroform, and proprionic acid) was used to fix immature heads for chromosome counts from the microsporocytes. Anther sacs from the disc florets were macerated in 2 percent acetic-lactic orcein stain and squashed. Selected slides were made permanent using the dry-ice technique and mounting in Euparol or CM-10. Root tips from germination seedlings were used for checking chromosome determinations and for attempting to provide karotype information. The species attempted were Heterotheca graminifolia, H. microcephala, H. ruthii, H. adenolepis, H. oligantha, and H. flexuosa. Excised root tips were placed in 0.3 percent 8-hydroxyquinoline for 4 hours at room temperature, hydrolyzed using Orcein-HCl (9:1) solution for 10-15 minutes while heating three to four times, and then stained for 30 minutes in 45 percent aceto-orcein stain (modified from Harms, 1963). The cells are then squashed and preserved as above.

To test for self-fertility and apomixis, flowers on

plants in the greenhouse were bagged to exclude pollinators using nylon stockings over a frame supported by poles. The bags were kept on until seed set could be determined. This bagging method was used also to provide a method to test compatibility within species and also to attempt hybrid crosses. These crosses were made normally by rubbing flower heads together when the anther sacs were apparently mature. The flowers were kept bagged until the achenes were mature. The hybrid seedlings that survived were grown to maturity and where possible were analyzed for morphological characters, cytological results, and pollen fertility. Some of the hybrids were backcrossed with their parents.

An attempt was made to study flavonoid compounds found in section Pityopsis and also available species in sections Heterotheca and Chrysopsis. Voucher specimens will be deposited in The University of Tennessee Herbarium, Knoxville.

Techniques are similar to those found in Mabry, Markham, and Thomas (1970). Extracts were prepared from dried, crushed leaves and also from flower head extracts. Four to five specimens for each species of section Pityopsis were used for extract material for separate runs to provide comparison material. Flavonoids were extracted overnight in 85 percent methanol. This was spotted on

Whatman 3 MM chromatographic paper and chromatograms developed in solvent systems (3:1:1 v/v) of t-butonol, glacial acetic acid, and water for the first dimension and 15 percent glacial acetic acid for the second dimension. The resulting spots were then read for Rf values while viewing under ultraviolet light and then under ultraviolet light with ammonia vapors for color characteristics.

Over 3,500 specimens from 18 regional and national herbaria were studied to provide information on variation patterns and to provide distribution data. All herbarium specimens in this study were examined and will be annotated. Where collections of the author were not adequate in number or in geographic areas not collected, selected specimens were studied in detail. This varied with the species such as all studied in Heterotheca ruthii (19 specimens) to a small portion in Heterotheca graminifolia (less than 40 of a total of 800 specimens available). Other species were examined selectively as needed.

Loans were provided from the Wiegard Herbaria at Cornell University (CU), Duke University (Duke), Field Museum, Chicago (F), Florida State University (FSU), University of Georgia (GA), Gray Herbarium of Harvard University (GH), University of Kansas (KANU), University of Southwestern Louisiana (LAF), Louisiana State University

(LSU), University of Michigan (MICH), Missouri Botanical Gardens (MO), University of North Carolina (NCU), New York Botanical Garden (NY), Academy of Natural Science at Philadelphia (PH), Southern Methodist University (SMU), University of Texas (TEX), National Museum at the Smithsonian Institution (US), University of South Florida (USF), and Vanderbilt University (VDB).

Types or photographs of types were obtained from the Gray Herbarium, New York Botanical Gardens, Academy of Natural Science at Philadelphia, and the following foreign Herbaria: Berlin (B), Leiden (L), and Paris (PC).

CHAPTER IV

RESULTS

General Morphology

The Heterotheca graminifolia group (H. graminifolia, H. microcephalia var. microcephala and var. aequilifolia, H. aspera, H. adenolepis, and H. oligantha) is a fairly cohesive group and will often be discussed together. The other species group, H. pinifolia group, includes H. pinifolia, H. falcata, H. flexuosa, and provisionally H. ruthii. Heterotheca ruthii frankly is intermediate between the two groups but is more closely related to the latter group than the former.

Heterotheca section Pityopsis taxa are all perennial with short, sometimes woody, rootstocks from which slender roots arise. Apparently all of the section has the ability to produce rhizomes of various lengths (except possibly H. microcephala var. aequilifolia). In the H. pinifolia group the rhizomes are shorter than the H. graminifolia group, ranging generally from 1-4 cm, occasionally longer. The rhizomes of the H. graminifolia group are from generally 7-20 cm in length. This can result in fairly large clones, especially apparent in Georgia and Florida portions of the ranges of the species.

The stems are herbaceous (occasionally nearly woody in central Florida in H. graminifolia and H. microcephala var. aequilifolia) somewhat striate, sometimes purplish, and variable in height, thickness, branching, and aspect. The pubescence and glands are of diagnostic importance in most species. Heterotheca pinifolia normally appears almost glabrate on the stem and peduncle but has minute tomentose pubescence under 10X magnification. Pubescence in the other species ranges from silvery sericeous to almost villous in certain species in the H. pinifolia group and varies with the species involved as to what portions are covered. There is a secondary pubescence (only tomentose in H. pinifolia) underneath the primary pubescence in H. falcata, H. flexuosa, and H. ruthii of short, light-colored tomentose hairs on the stem. The glands vary from many dark glands over most of the stem in H. oligantha to none in other species.

Section Pityopsis has either graminiform basal leaves which are longer than the cauline leaves in the H. graminifolia group or with the cauline leaves usually longer than the basal leaves and non-graminiform in the H. pinifolia group (intermediate in H. ruthii). The H. graminifolia group has basal leaves which are simple, sessile, clasping, with almost sheathing bases, attenuate, entire (glandular along the margin in H. aspera), and appressed soft-sericeous (sometimes glabrate with age). The cauline leaves in this

group are similar to the basal except that they are rapidly reduced in width and length upward (except in H. microcephala var. aequilifolia which has sub-equal cauline leaves. Heterotheca aspera often has upper leaves which are glabrate but in shape are similar to the others in the group. The H. pinifolia group has cauline leaves which are not reduced rapidly in size and in fact often become longer than the basal leaves, and which vary from filiform, linear, linear-falcate, to oblong-lanceolate. There pubescence on the cauline leaves ranges from silvery-sericeous (H. ruthii) to almost glabrate. They are entire.

The inflorescence of the H. graminifolia group is corymbiform to cymose-paniculate except for H. oligantha which is openly cymose with few heads on long, slender peduncles. The inflorescence of the H. pinifolia group ranges from being strictly terminal to those that are branched and cymose paniculate. Peduncles in this section may be almost glabrate to glandular or pubescent (or both) and are important taxonomically. Heads vary in size in the H. graminifolia group tetraploids (H. oligantha and H. graminifolia) usually being larger (more than 8 mm) than the smaller headed (less than 7 mm) diploid, H. microcephala var. microcephala and H. aspera. The other group are all diploids and the heads vary in size but are larger than those of the two diploids in the graminifolia group.

Head number may range in both groups from a few (3-10) in H. oligantha to over 150 in H. microcephala and H. adenolepis. Phyllary pubescence and glandularity varies from almost arachnoid to glabrate, with intermediate stages of being glandular or sericeous pubescent. The H. pinifolia group may be almost glabrate (H. pinifolia), or pubescent only (H. falcata and H. flexuosa), or glandular (H. ruthii). The H. graminifolia group generally can be glandular, glandular and pubescent, or sericeous pubescent only. The character is useful in certain taxa especially in determination of possible hybrids. The number and size of disc corolla are useful in determining certain species, especially in H. graminifolia and H. microcephala. Other taxonomically useful characters are length of limb (ray or ligulate flowers) and their number, anther sac length, and length of the stigmatic papillae. Features such as disc flower lobe length, outer and inner pappus length, achene length and pubescence, receptacle shape, measured on several hundred specimens have not appeared to be consistent or show enough difference for diagnostic usefulness.

Plants in the greenhouse did not differ significantly from plants in the field except that Heterotheca graminifolia and H. oligantha which produced exceptionally long (70-80 cm) basal leaves under long-day conditions.

Cytological Variation

In Table III the results of the cytological determinations are given. Some of the counts are derived from collections in the field and others from greenhouse transplants. No local variation was found so no more than one entry is made per location. Only in H. adenolepis are there diploid and tetraploid races. The chromosome drawings found in Figure 1 are from entities in section Pityopsis.

The summary of pollen size and stainability is found in Table IV. The difference in diploid and tetraploid size is not apparently significant in H. adenolepis. In certain cases pollen size could be important for separating H. microcephala (N=9) and H. graminifolia (N=18) as shown in Figure 2.

Chemotaxonomic Studies

A total of 23 comparable compounds were obtained from the extracts of species in Heterotheca section Pityopsis and selected species in sections Heterotheca and Chrysopsis as listed in Table V. The total pattern of spots obtained is shown in Figure 3, and their colors under ultraviolet and UV with ammonia vapor in Table VI. Most of them appear to be flavonoid compounds as described in Mabry, Markham, and Thomas (1970). Rf or gradient value was determined by making a grid and placing over the paper after a run, and this

TABLE III

CHROMOSOME NUMBERS IN *HETEROTHECA* SECT. *PITYOPSIS*

Species	Number	Location and Voucher
H. adenolepis	9	MISS. Lamar Co.: Jones #3502
	9	N.C. Moore Co.: Bowers #70-109
	18	FLA. Escambia Co.: Bowers #72-270
	18	FLA. Escambia Co.: Bowers #72-275
	18	GA. Taylor Co.: Bowers #71-562
	18	GA. Thomas Co.: Bowers #70-470
	18	N.C. Burke Co.: Bowers #72-230
	18	N.C. McDowell Co.: Bowers #72-232
	18	N.C. Montgomery Co.: Bowers #70-101
	18	VIRG. James Co.: Bowers #72-220
	18	VIRG. Southhampton Co.: Bowers #72-228
H. aspera	9	FLA. Leon Co.: Bowers #70-481
	9	FLA. Hamilton Co.: Bowers and Wofford #71-561
H. falcata	9	N.J. Atlantic Co.: Bowers and Bowers #72-210
	9	N.J. Burlington Co.: Bowers and Bowers #72-215
	9	N.J. Ocean Co.: Bowers and Bowers #72-205
	9	N.J. Ocean Co.: Morton n.s.
H. flexuosa	9	FLA. Leon Co.: Bowers #70-484
H. graminifolia	18	ALA. Baldwin Co.: Bowers #71-202
	18	FLA. Duvall Co.: Morton #4626
	18	FLA. Leon Co.: Bowers #70-482
	18	N.C. Bladen Co.: Bowers #71-490
	18	N.C. Columbus Co.: Bowers #71-465
	18	TENN. Pickett Co.: Bowers #69-305
	18	TENN. Polk Co.: Bowers #71-581
	18	TENN. Roane Co.: Bowers #69-301
H. microcephala	9	ALA. Baldwin Co.: Bowers #72-203
	9	ARK. Ashley Co.: Bowers #72-250
	9	ARK. Ashley Co.: Bowers #72-255

TABLE III (continued)

Species	Number	Location and Voucher
	9	ARK. Drew Co.: Bowers #72-240
	9	FLA. Alachua Co.: Bowers #72-550
	9	FLA. Escambia Co.: Bowers #72-278
	9	FLA. Hamilton Co.: Bowers and Wofford #71-561-e
	9	FLA. Leon Co.: Bowers #70-481
	9	FLA. Volusia Co.: Bowers and Wofford #71-553
	9	MISS. Hancock Co.: Bowers #72-260
H. microcephala var. aequilifolia	9	FLA. Lake Co.: Bowers and Wofford #71-557
	9	FLA. Lake Co.: Bowers and Wofford #71-558
	9	FLA. Manatee Co.: Bowers and Wofford #71-559
H. oligantha	18	ALA. Baldwin Co.: Bowers #71-201
	18	FLA. Liberty Co.: Bowers #72-120
	18	FLA. Wakulla Co.: Bowers #72-117
H. pinifolia	9	GA. Taylor Co.: Bowers and Wofford #72-562-a
	9	N.C. Moore Co.: Bowers #70-110
H. ruthii	9	TENN. Polk Co.: Bowers #71-580
	9	TENN. Polk Co.: Bowers and Odenwelder #45573

Figure 1. Traced drawings from photographs of chromosomes of Heterotheca species. All at metaphase I. (Location data in Table III, page 24). Numbers are author's collections unless otherwise noted.

A. H. microcephala var. aequilifolia (#71-558).

B. H. falcata (#72-220).

C. H. pinifolia (#71-563).

D. H. microcephala var. microcephala (#70-202).

E. H. aspera (#70-205).

F. H. flexuosa (#71-95).

G. H. ruthii (#45573 Bowers and Odenwelder).

H. H. adenolepis (#71-562-b).

I. H. graminifolia (#4626 Morton).

J. H. adenolepis (#72-232).

K. H. oligantha (#71-201).

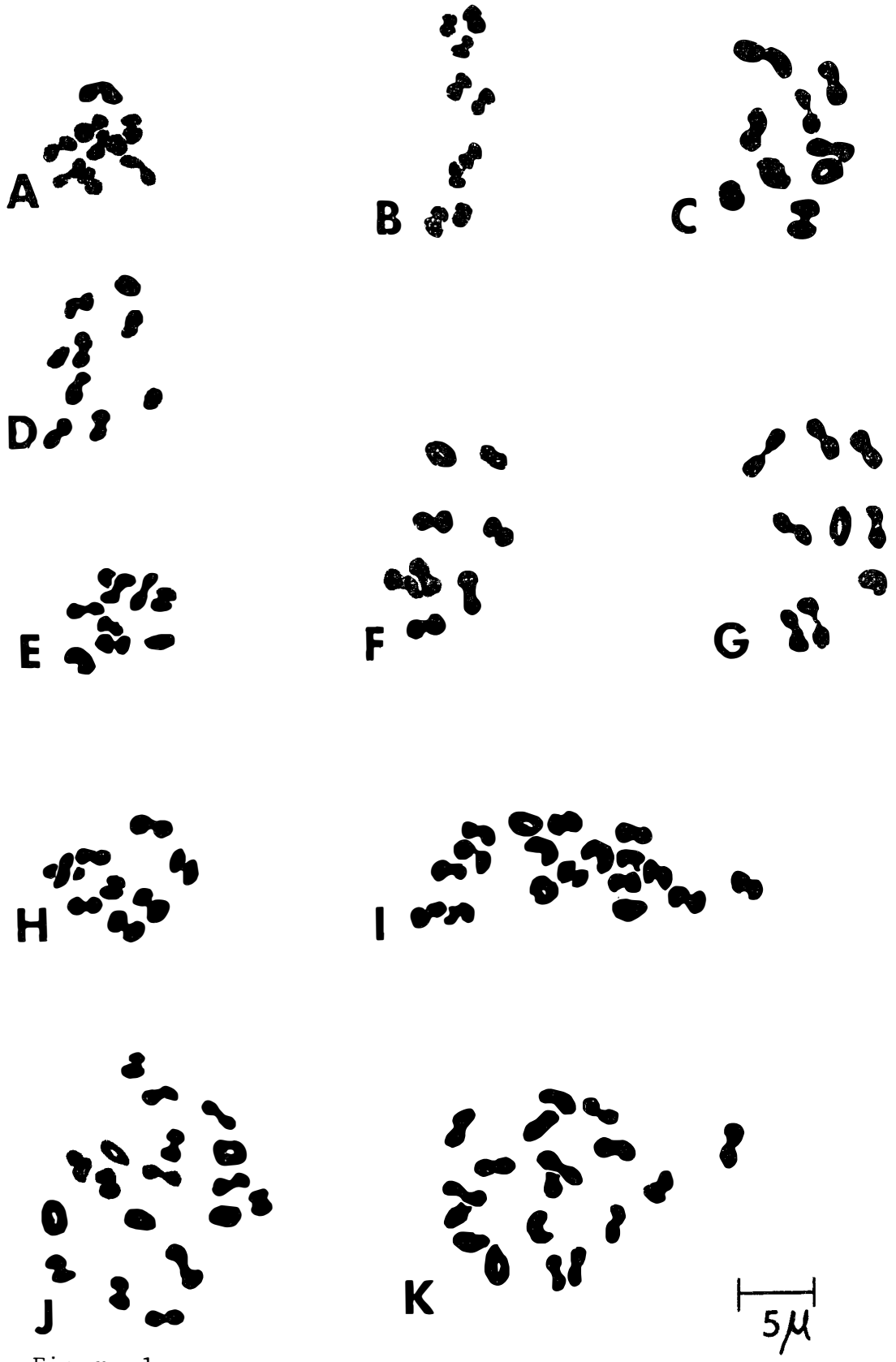

Figure 1

TABLE IV

POLLEN SIZE AND STAINABILITY

Species	Location and Voucher	Mean Size μ	Size Range μ	Percent Stainable
H. adenolepis N=9	MISS.:			
	Lamar Co., Jones #3502	17.4	16.0-19.7	88.0
	N.C.:			
	Moore Co., Bowers #70-109	19.4	18.3-20.8	97.3
		18.2	16.4-19.9	97.0
		18.3	17.4-19.9	99.1
		19.5	17.7-20.8	99.6
		20.2	18.8-21.8	96.4
		19.4	18.2-20.9	98.0
		19.5	18.6-20.9	94.6
		18.5	16.3-20.2	97.4
		17.8	16.7-19.1	99.3
H. adenolepis N=18	FLA.:			
	Leon Co., Bowers #71-479	19.8	17.8-22.0	98.7
		19.7	17.5-21.8	97.2
	GA.:			
	Taylor Co., Bowers #71-562	20.3	18.7-22.0	93.6
		20.5	18.9-21.9	95.0
		19.8	17.8-21.2	93.9
	N.C.:			
	Montgomery Co., Bowers #45559	20.0	18.5-21.7	83.2
		20.8	19.4-22.2	91.4
	Montgomery Co., Bowers #45560	20.4	18.9-22.1	98.7
		19.6	18.0-20.9	98.2
	Moore Co., Bowers #45554	20.8	19.1-22.1	99.3
H. aspera	FLA.:			
	Hamilton Co., Bowers and Wofford #71-561	20.0	18.9-21.5	98.3
		18.7	17.6-20.0	87.8
	Jefferson Co., Godfrey #70073	19.0	17.7-19.9	95.8

TABLE IV (continued)

Species	Location and Voucher	Mean Size μ	Size Range μ	Percent Stainable
	Leon Co., Bowers #70-481	17.6	16.6-18.9	99.7
		19.0	17.7-20.0	99.0
		17.6	16.5-18.8	98.3
		17.5	16.5-18.0	90.0
		17.6	16.6-18.8	99.2
		18.6	17.8-19.8	97.8
	Wakulla Co., Godfrey #70073	19.0	17.5-19.7	96.2
H. falcata	MASS.:			
	Barnstable Co., Eames #48	19.8	19.1-21.1	95.8
	N.J.:			
	Atlantic Co., Bowers #72-210	19.1	17.6-20.8	87.2
	Burlington Co., Bowers #72-215	18.6	16.6-19.8	89.2
		18.7	16.6-20.7	90.0
	Ocean Co., Bowers #72-205	19.4	17.6-20.1	83.2
	Ocean Co., Morton #2132	18.7	17.4-20.0	91.2
	Ocean Co., Morton s.n.	20.4	19.3-21.8	98.0
	Ocean Co., Morton s.n.	19.7	18.3-21.1	97.0
	Ocean Co., Morton s.n.	19.8	17.7-20.1	99.0
	N.Y.:			
	Muenscher and Curtis #6557	18.3	17.2-19.8	98.0
H. flexuosa	FLA.:			
	Leon Co., Bowers #70-484	20.0	18.2-21.2	96.7
		19.8	17.7-21.3	96.0
		19.1	17.4-21.0	96.0
		19.2	17.3-21.0	95.8
		19.4	17.7-20.9	99.1
		19.7	17.6-21.0	67.2
		19.0	17.2-20.7	99.5
		19.2	17.6-21.0	97.2
	Leon Co., Lazor #5132	19.4	17.4-21.0	97.6
	Wakulla Co., Godfrey #70072	19.0	17.5-20.8	97.3

TABLE IV (continued)

Species	Location and Voucher	Mean Size μ	Size Range μ	Percent Stainable
H. graminifolia	ALA.:			
	Baldwin Co., Bowers #71-201	24.1	22.6-26.2	82.0
	Jackson Co., Morton #4105	23.5	22.4-25.0	97.0
	FLA.:			
	Duval Co., Morton #4105	23.5	22.1-25.1	97.0
	GA.:			
	Chatooga Co., Morton #4162	23.8	22.4-25.1	99.3
	Floyd Co., Morton #4145	22.8	18.9-24.3	94.0
	N.C.:			
	Columbia Co., Bowers #71-490	23.8	22.4-25.4	96.3
	TENN.:			
	Campbell Co., Sharp #46853	24.2	23.5-25.1	99.3
	Morgan Co., Bowers #70-460	24.2	22.0-26.5	96.4
	Pickett Co., Bowers #69-305	23.1	21.3-24.6	98.3
	Polk Co., Bowers #71-581	23.0	20.9-24.3	99.2
H. microcephala var. microcephala	ALA.:			
	Baldwin Co., Bowers #71-202	20.2	18.8-21.8	87.0
	ARK.:			
	Asheley Co., Bowers and Bowers #72-255	18.0	15.8-19.9	92.4
		18.2	16.4-20.0	93.2
		18.4	16.3-20.1	95.3
	Drew Co., Bowers and Bowers #72-240	18.5	16.9-19.6	76.1
	FLA.:			
	Hamilton Co., Bowers and Wofford #71-561-d	20.1	18.7-21.3	95.6

TABLE IV (continued)

Species	Location and Voucher	Mean Size μ	Size Range μ	Percent Stainable
	Thomas Co., Godfrey #70103	19.3	17.3-20.2	90.0
	Volusia Co., Bowers and Wofford #71-553	18.8	16.7-19.9	96.2
	GA.:			
	Thomas Co., Morton #2672	19.4	17.8-20.2	99.0
	MISS.:			
	Pearl River Co., Morton #4307	17.9	16.5-19.9	98.0
H. microcephala var. aequilifolia	FLA.:			
	Lake Co., Bowers and Wofford #71-557	18.5	17.5-19.6	97.0
	Lake Co., Bowers and Wofford #71-558	19.7	18.9-20.9	96.0
		19.9	18.6-20.8	93.2
		18.9	17.4-20.8	97.8
		17.9	17.4-19.3	98.2
		18.4	14.7-20.2	95.0
	Manatee Co., Bowers and Wofford #71-559	18.6	17.7-19.6	95.2
	Marion Co., Bowers #71-560	19.1	17.8-20.8	96.6
		18.1	16.5-19.8	93.0
H. oligantha	ALA.:			
	Baldwin Co., Bowers #71-201	24.9	24.1-25.6	96.2
		23.5	22.1-25.1	92.0
		22.5	21.1-24.2	91.6
		22.8	20.9-24.2	92.3
	Geneva Co., Kral #31371	23.0	21.3-25.3	93.0
	FLA.:			
	Liberty Co., Bowers #72-120	23.0	22.0-25.3	99.3
		24.1	21.8-26.3	99.0
		22.8	21.0-24.2	97.2
	Liberty Co., Godfrey #68489	22.6	21.3-24.0	98.0
	Wakulla Co., Clewell #1674	22.6	20.6-25.4	99.0

TABLE IV (continued)

Species	Location and Voucher	Mean Size μ	Size Range μ	Percent Stainable
H. pinifolia	GA.:			
	Taylor Co., Bowers and Wofford #71-562	19.1	17.8-20.4	97.8
		19.5	18.2-20.6	77.1
		17.8	16.6-19.9	51.4
		19.6	18.0-20.7	91.4
		19.8	17.8-21.1	97.6
	N.C.:			
	Harnett Co., Radford #45276	20.0	18.8-21.3	87.2
	Moore Co., Bowers #70-108	19.2	16.5-19.8	88.7
	Moore Co., Godfrey #50115	20.4	18.9-21.3	97.8
	Richmond Co., Duke #2481	19.3	18.7-20.1	96.3
	Wayne Co., Godfrey and Fox #50634	18.7	17.4-19.9	96.8
H. ruthii	TENN.:			
	Polk Co., Bowers #71-580	20.2	18.0-22.2	93.8
		20.2	19.1-21.1	98.2
		19.4	18.0-21.3	91.8
		19.6	17.7-21.3	96.9
		18.4	17.4-20.2	98.8
		18.7	16.6-19.6	98.9
		19.0	17.7-20.2	99.0
		18.7	16.5-19.9	97.3
		18.4	16.3-19.9	98.3
	Polk Co., Bowers and Odenwelder #45573	19.6	17.6-21.5	91.7

Figure 2. Pollen sizes of Heterotheca section Pityopsis showing mean size, standard deviation, and range.

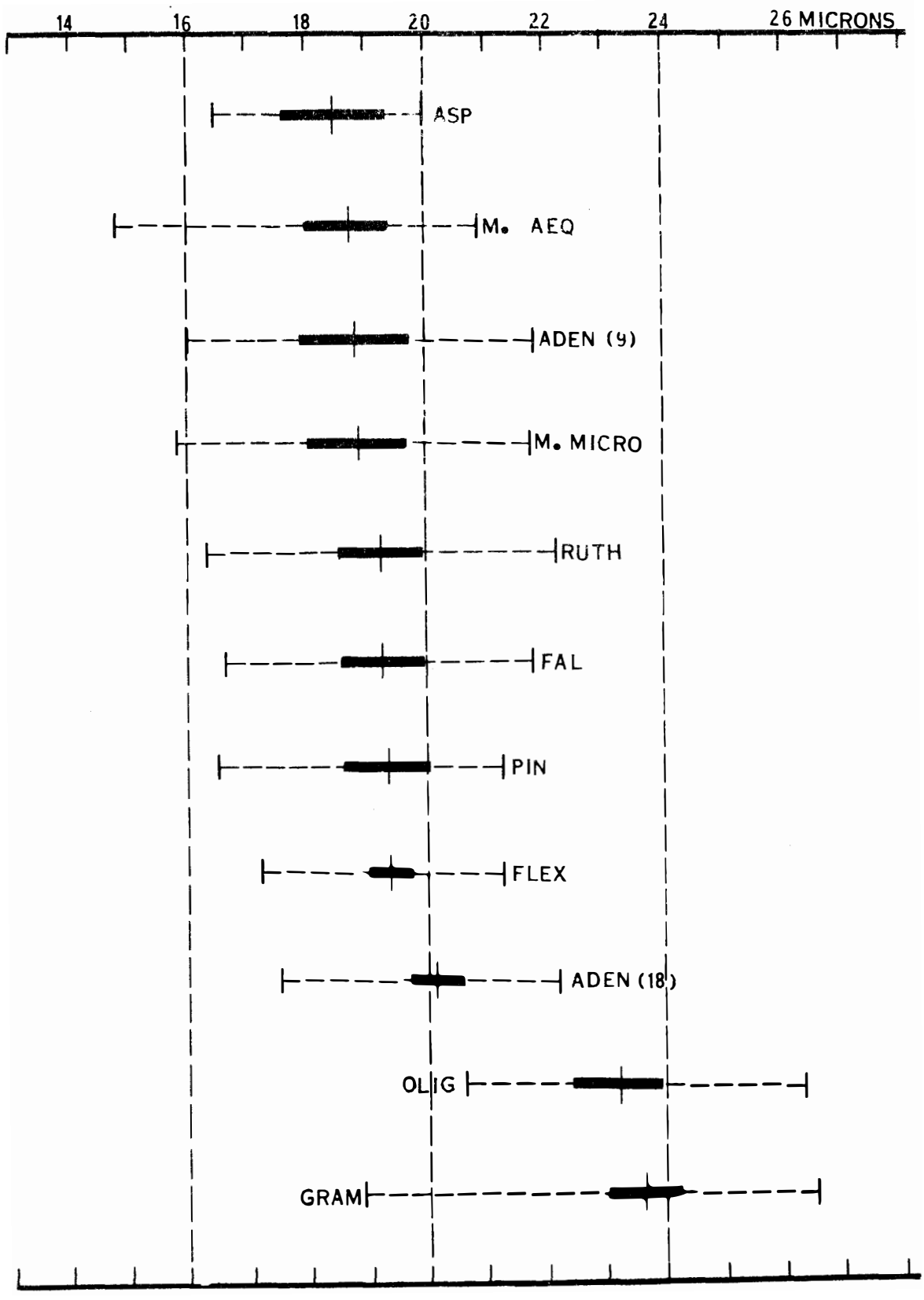
14
16
18
20
22
24
26 MICRONS
ASP
M. AEQ
ADEN (9)
M. MICRO
RUTH
FAL
PIN
FLEX
ADEN (18)
OLIG
GRAM

Figure 2

TABLE V

POPULATIONS OF HETEROTHECA EXAMINED FOR FLAVONOIDS BY PAPER CHROMATOGRAPHY

Species	Collection Data
Sect. Chrysopsis	
H. camporum	TENN. Hardeman: McConnell s.n.
H. pilosa	FLA. Alachua Co.: Bowers and Wofford #71-562-a
H. villosa	ARK. Boone Co.: Bowers #72-235
Sect. Heterotheca	
H. latifolia	MISS. Hancock Co.: Bowers #72-261
H. subaxillaris	TENN. Knox Co.: Bowers #72-280
Sect. Pityopsis	
H. adenolepis	N.C. Moore Co.: Bowers #70-109
H. aspera	FLA. Hamilton Co.: Bowers and Wofford #71-561-a
H. falcata	N.J. Ocean Co.: Bowers and Bowers #72-205
H. flexuosa	FLA. Leon Co.: Bowers #70-484
H. graminifolia	TENN. Roane Co.: Bowers #69-301
H. micro	FLA. Hamilton Co.: #71-561-e
H. micro var. aequilifolia	FLA. Marion Co.: Bowers and Wofford #71-560
H. pinifolia	GA. Taylor Co.: Bowers and Wofford #71-562
H. ruthii	TENN. Polk Co.: Bowers #71-580

Figure 3. A composite chromatogram of species of Heterotheca. Colors and Rf values appear in Table VI, page 38.

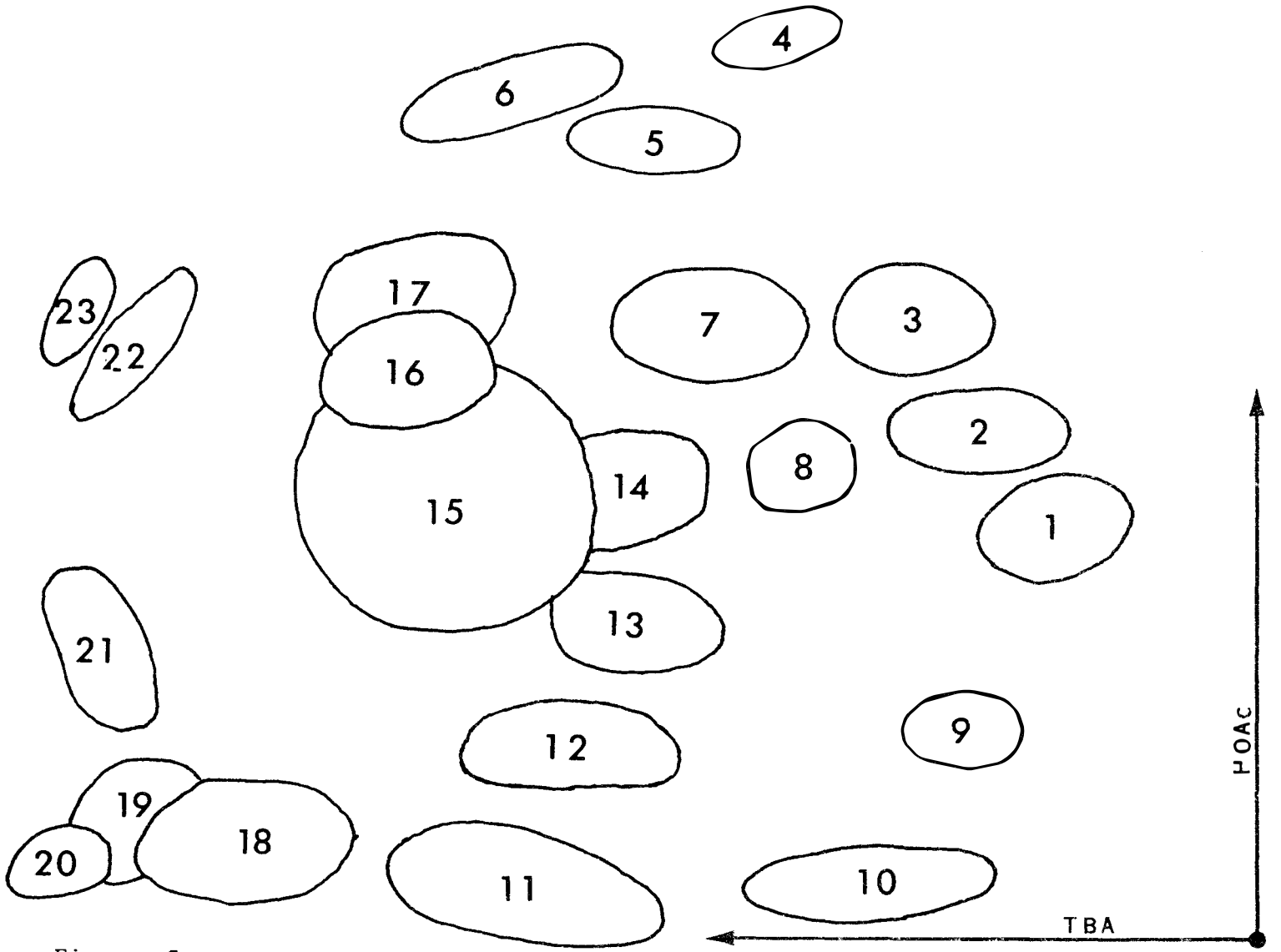

Figure 3

TABLE VI

CHROMATOGRAPHIC PROPERTIES OF COMPOUNDS OF HETEROTHECA SECTION PITYOPSIS AND SELECTED OTHER SPECIES OF SECTIONS CHRYSOPSIS AND HETEROTHECA

Spot Number	Color		Rf Values	
	U.V.	+NH_3[a]	TBA	HOAC
1	P	YGr	.14	.43
2	P	Gr	.20	.48
3	P	YGr	.23	.55
4	B	B	.30	.80
5	B	B	.42	.78
6	LB	LGr	.47	.74
7	P	YGr	.29	.54
8	P	YGr	.32	.48
9	P	DkGr	.15	.25
10	Y	Y	.26	.02
11	Y	Y	.38	.02
12[b]	Gr	Gr	.43	.22
13	P	YGr	.43	.29
14	P	DkGr	.38	.42
15	LB	LGr	.55	.38
16	Gr	DkGr	.55	.54
17	LB	LB	.57	.60
18	P	DkGr	.61	.07
19	P	O	.72	.10
20	P	RP	.74	.02
21	P	LGr	.72	.25
22	P	LGr	.70	.54
23	B	FlB	.74	.55

[a]Dk = dark; Y = yellow; B = blue; Gr = green; P = purple; Fl = fluorescent; L = light; O = orange; R = red.

[b]Spot 12 is present only in flowers.

information is also in Table VI. Species spots are shown in Figures 4, 5, and 6.

Limited success was apparent in that certain species appeared closely related as indicated by the high number of spots in common. Apparently in other compositae many more differences have been found within species, for example, by Bierner (1971) and Powell (1969). Species H. aspera, H. microcephala (both varieties), H. flexuosa, H. adenolepis, and H. pinifolia contained a large number of similar spots and using a "Paired Affinity Index*," Table VII, (Radford, et al., 1972) the similarity ranged from 60 percent to 80 percent affinity. Heterotheca graminifolia and H. oligantha had a lesser number of spots but in common shared a 75 percent affinity. Heterotheca falcata and H. ruthii had the least number of spots but a 77 percent affinity. While the above results compare fairly well with other evidence for relationship, the two species, H. pinifolia and H. flexuosa, have been found to be usually more closely related to H. ruthii and H. falcata (using other evidence). One spot common to H. flexuosa, H. aspera, and H. adenolepis was number 21 which is also found in certain species of sections Heterotheca and Chrysopsis (Figure 4).

---

*PA = $\frac{\text{Characters in common for species A and B}}{\text{Total characters for A + B}} \times 100$

Figure 4. Chromatographic profiles of Heterotheca species (including species in section Chrysopsis and Heterotheca).

A. H. camporum (section Chrysopsis) and H. subaxillaris (section Heterotheca) (dark circles, H. camporum only; dotted circles, H. subaxillaris only; other circles present in both species).

B. H. pilosa (section Chrysopsis).

C. H. graminifolia.

D. H. oligantha.

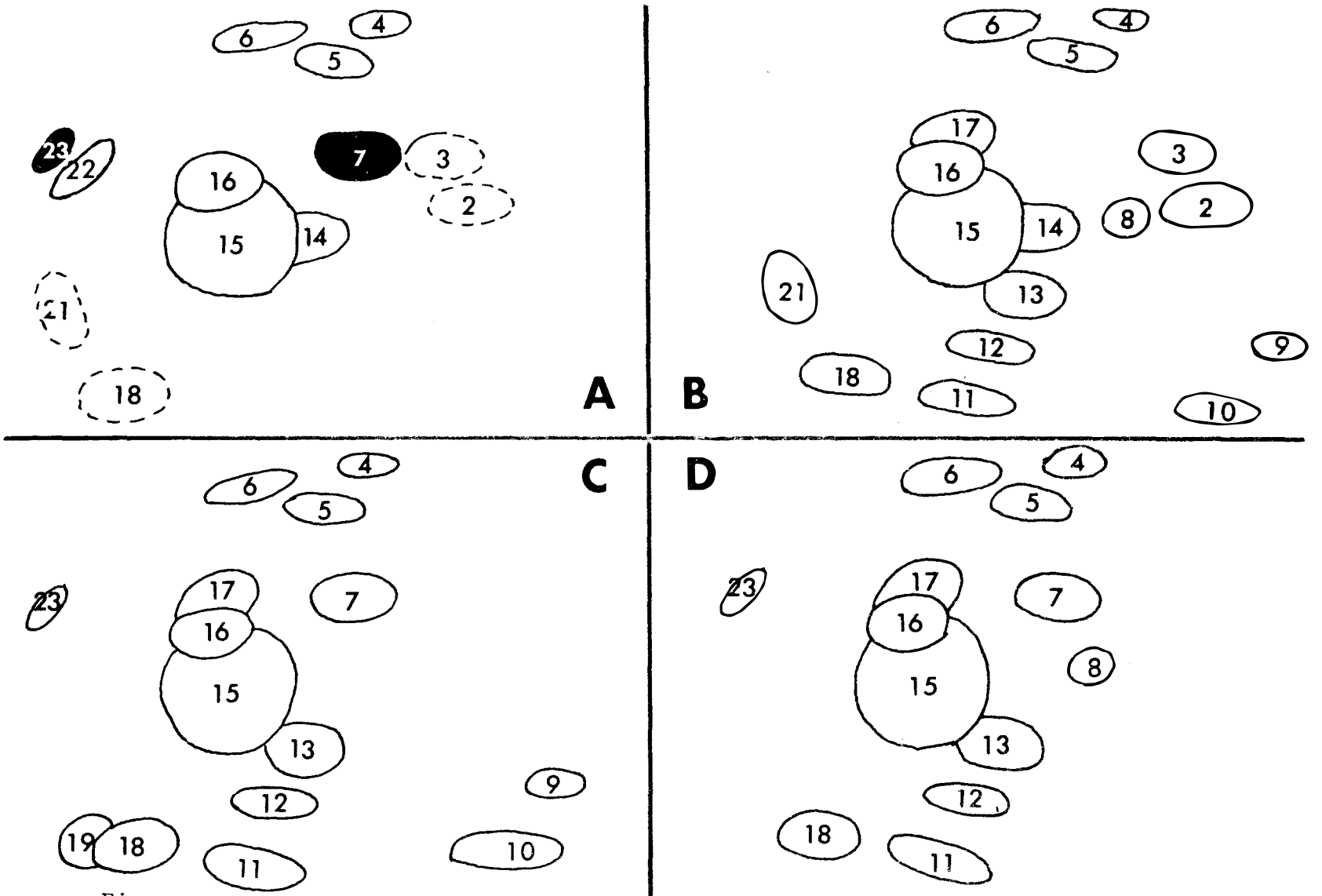

Figure 4

Figure 5. Chromatographic profiles of Heterotheca species (Heterotheca graminifolia group).

A. H. microcephala var. aequilifolia.

B. H. microcephala var. microcephala.

C. H. adenolepis.

D. H. aspera.

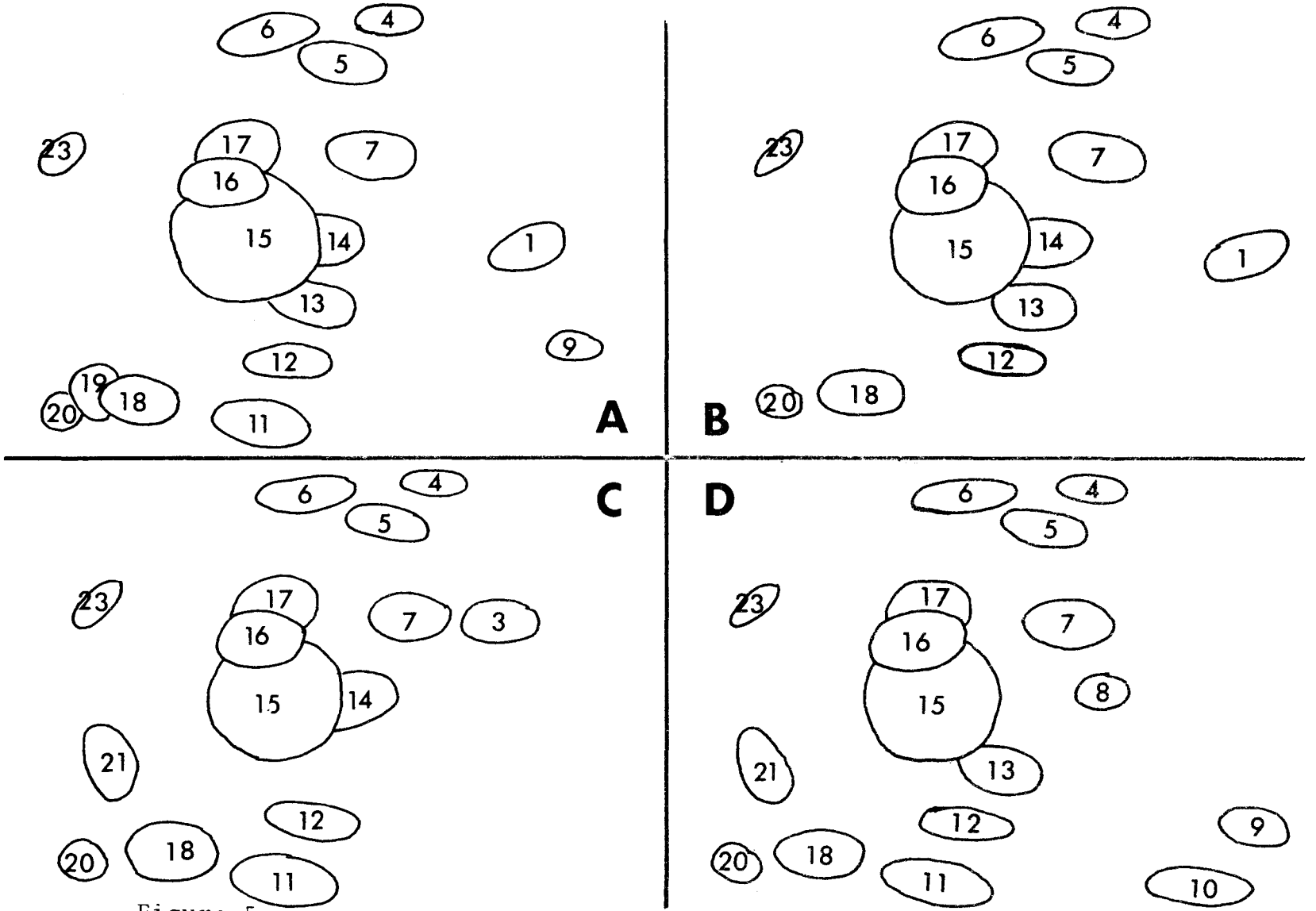

Figure 5

Figure 6. Chromatographic profiles of Heterotheca species (Heterotheca pinifolia group).

A. H. pinifolia.

B. H. ruthii.

C. H. falcata.

D. H. flexuosa.

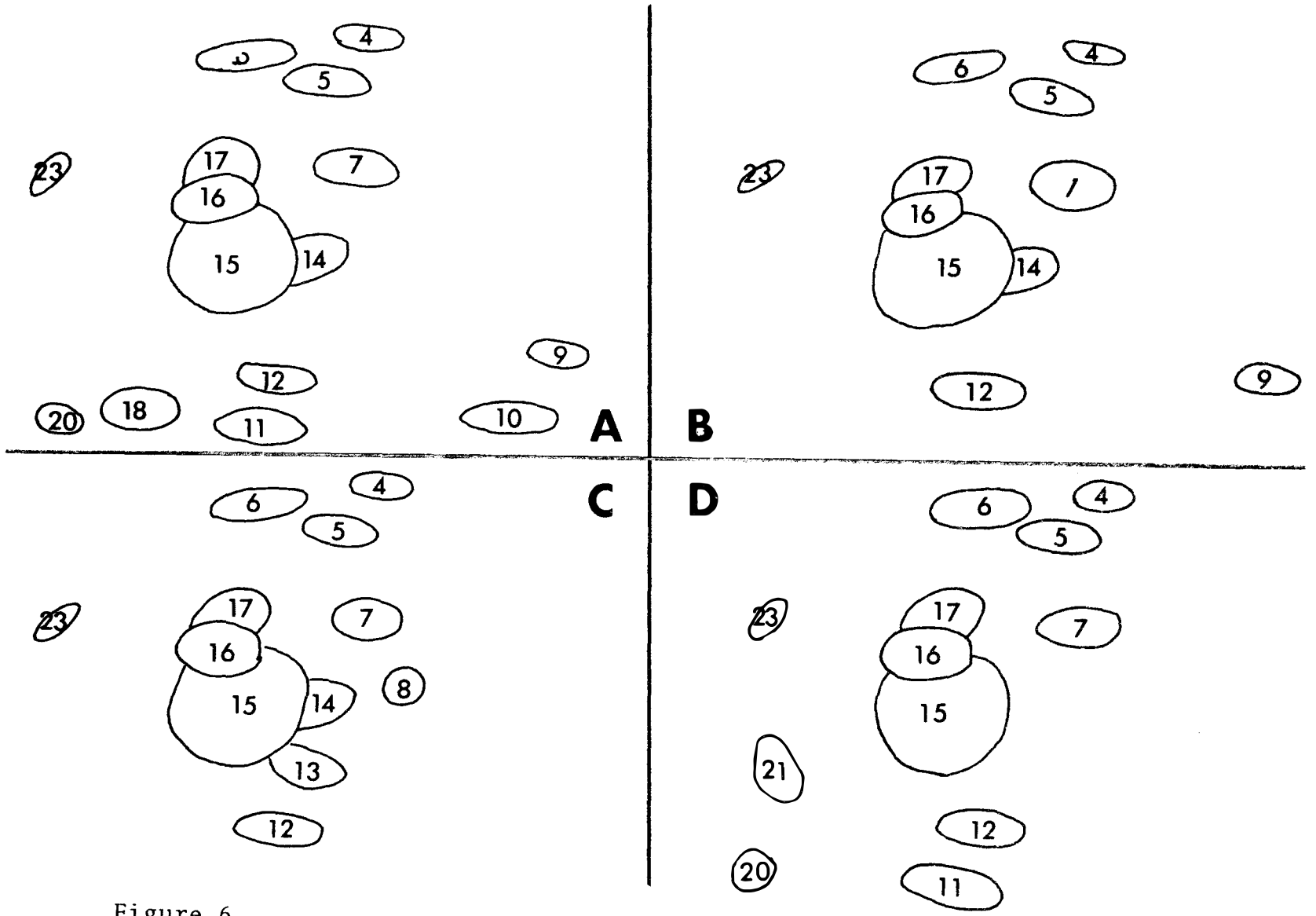

Figure 6

TABLE VII

CHROMATOGRAPHIC PAIRED AFFINITY VALUES OF HETEROTHECA TAXA

Taxa	Pil	Camp	Subax	Gram	Olig	Aden	Asp	Micro Micro	Micro Aeq	Fal	Flex	Pin	Ruth
Pilosa	100												
Camporum	30	100											
Subaxillaris	56	54	100										
Graminifolia	57	41	30	100									
Oligantha	58	54	33	75	100								
Adenolepis	60	57	53	55	64	100							
Aspera	70	57	33	78	76	68	100						
Microcephala var. microcephala	49	53	47	55	69	70	63	100					
Microcephala var. aequilifolia	55	44	40	78	60	68	70	82	100				
Falcata	53	61	35	50	79	59	61	73	61	100			
Flexuosa	45	54	37	53	66	80	70	63	61	53	100		
Pinifolia	60	44	40	76	64	76	78	70	78	59	69	100	
Ruthii	47	66	37	58	64	63	56	66	77	77	64	73	100

Heterotheca pilosa (section Chrysopsis) had an affinity value of 70 percent with H. aspera and thus appeared to have more spots in common with section Pityopsis than with section Chrysopsis (H. camporum - 30 percent) or section Heterotheca (H. subaxillaris - 56 percent). Heterotheca subaxillaris (section Heterotheca) had a fewer number of total spots, but its greatest affinities were with H. adenolepis, H. microcephala, and H. camporum. Heterotheca camporum (section Chrysopsis), while lacking many of the spots, did have two which showed up only in section Pityopsis--numbers 23 and 7.

All the plants exhibited spots 4, 5, 6, 15 and 16. All the section Pityopsis plants had spot number 23 with only H. camporum showing it in the other two sections. This was absent also in H. mariana, H. villosa (in section Chrysopsis), and H. latifolia (section Heterotheca), but not enough extracts were sampled to include these taxa here.

This investigation is only preliminary but appears to show that at least three of the four sections of Heterotheca have many compounds in common. When more of the species in sections other than Pityopsis are sampled, this possibly could provide further evidence on phylogeny within the genus. Section Ammodia was not chromatographed in this study.

Breeding System

Tests for self-compatibility and apomixis in all

species were negative throughout the blooming seasons of the test periods. The bagged heads, when not pollinated with foreign pollen, produced no seed. Some problems occurred in attempting hybrids especially with Heterotheca falcata due to its early flowering time and susceptibility to mold when bagged. Some fungal problems also occurred in the other short stature species as H. ruthii and H. flexuosus when bagged. However, it appears from the evidence that both the H. graminifolia group and H. pinifolia group are normally outbreeding populations and that rarely does self-fertilization or apomixis take place, if at all.

In the field, bees of various types were seen to visit the flowers of section Pityopsis. In the greenhouse flies were seen occasionally visiting flowers. However, no study was made of insect pollinators. Probably wind pollination is of little importance in this group.

Hybridization Experiments

The hybridization attempts in section Pityopsis began in 1969 before adequate knowledge of the cytology was attained. However, in the summer of 1971 a number of crosses were attempted and quite a few were successful. As the seedling F_1 progeny are now maturing, no analysis of F_2 plants has been made, although backcrossing with the parents is being attempted with the F_1 progeny.

The attempted crosses are shown in Figure 7. The dotted line shows an unsuccessful attempt; the single solid line indicates a successful cross; and the double line means an F_1 hybrid grown to flowering size. None of the diploid H. adenolepis were grown in the greenhouse as it was not realized until late in the study that there was a diploid entity in H. adenolepis. This entity, therefore, was omitted from the crossing chart.

Also in the case of H. falcata there was difficulty because of lack of adequate material, earliness of flowering and the fact that greenhouse grown plants did not readily produce flowers. For the H. microcephala var. aequilifolia crosses, only two plants were available late in 1971; and since they were recent transplants, it is quite probable this shock could have caused hybridization failure. Crossing studies involving these entities are continuing.

All attempts to hybridize species in section Pityopsis with species in section Chrysopsis (Heterotheca mariana, H. camporum, and H. gossypina) failed.

When viable achenes were produced, a high percentage (usually 80-100 percent) would germinate. In fact, only in H. falcata has there been any difficulty in germinating achenes. None of the greenhouse-produced seeds of H. falcata have germinated, whether hybrids or not.

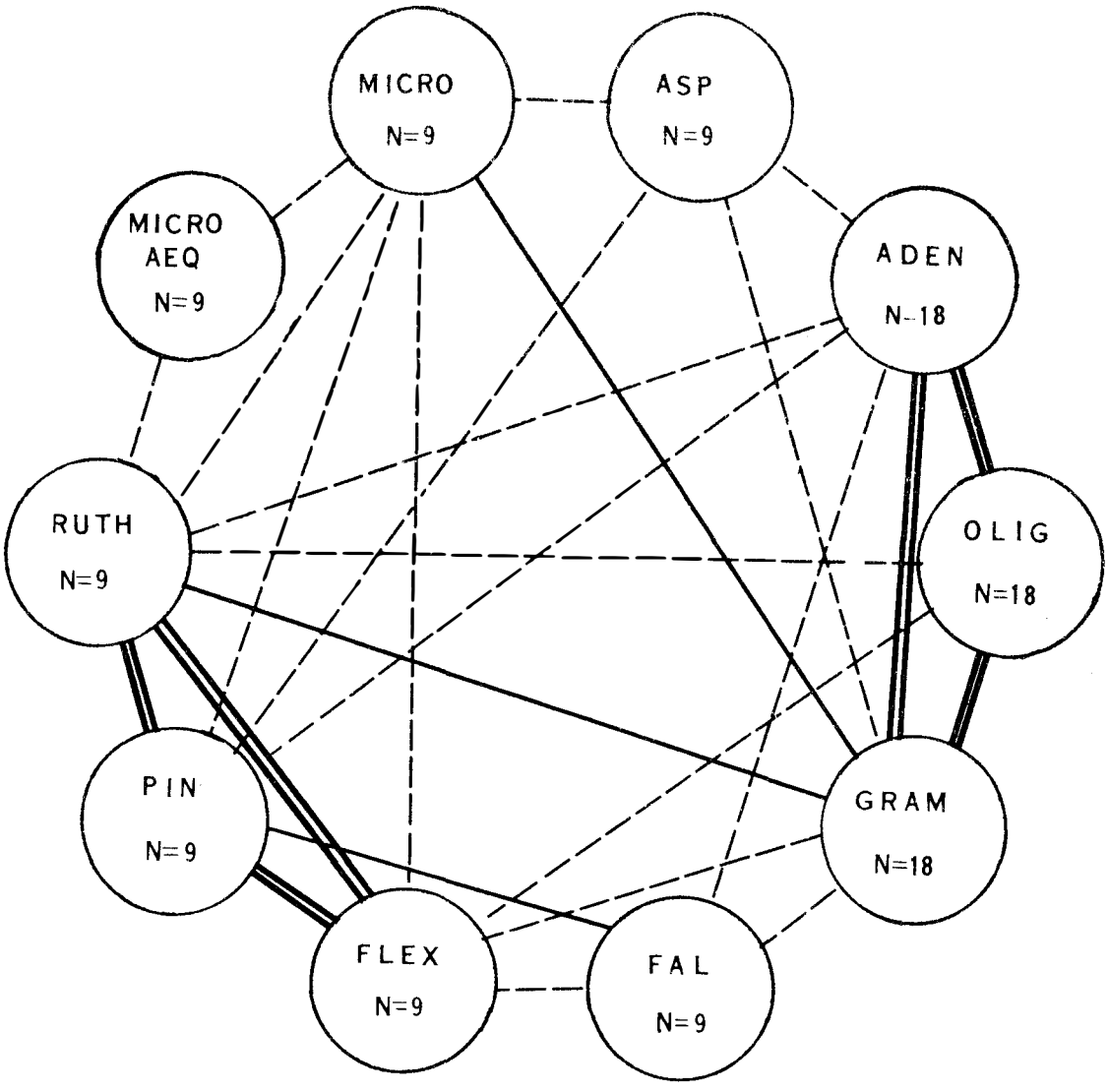

Figure 7. Artificial crosses in Heterotheca section Pityopsis. Dotted lines - unsuccessful crosses; solid lines - successful; double lines - F_1 grown to flowering size.

Cold treatments and dark and light treatments were attempted without success. Also treating seed with G.A. at rates of 500 to 1000 ppm which has been successful in other plants (Snider, 1969) was tried. In most cases various fungus infestation was seen soon after placing the seeds in sterilized petri dishes. Some of the achenes of H. falcata were treated with 95 percent alcohol and others with a solution of 1 percent chlorox. Although fungal attacks were limited, the seeds did not germinate.

Heterotheca adenolepis (N=18) x H. oligantha (N=18). Pollen stainability in the parents was high--over 90 percent in the former and over 97 percent in the latter. The F_1 hybrid had low stainability from less than 1 percent to about 5 percent inferred viability. Also, the observed pollen grains were badly misshapen, and the majority in structure being limited to the inner wall. While cytological examination showed no trivalents or univalents, much bridging did occur and the chromosomes tended to clump.

The F_1 hybrids appeared intermediate between the two plants. There were more cauline leaves than in H. oligantha and less than in H. adenolepis. The stem pubescence was more like H. oligantha. The head and flower size was intermediate between the two parents. The number of heads ranged from 6 to 24 which is nearer that of H. oligantha.

The peduncle length and number tended to be more like H. oligantha. The glands were light in color, unlike either parent.

Heterotheca graminifolia (N=18) x H. oligantha (N=18). The pollen stainability of both parents was high; usually over 97 percent. The pollen stainability in the F_1 hybrid ranged from 70.1 to 88.2 percent. There were a number of misshapen grains, but these were mostly stained positively. The chromosomes appeared to pair normally with less apparent bridging than the H. adenolepis x H. oligantha cross.

This cross was somewhat varied in the traits observed. The stem pubescence was similar to that of H. graminifolia. The peduncles were glandular like H. oligantha. The cauline leaf number was intermediate. The head number ranged from 4 to 7 and was more like that of H. oligantha. As the two parents are similar in head and flower size, no differences were noted.

Heterotheca graminifolia (N=18) x H. ruthii (N=9). Only two seeds were produced, one of which germinated and died about a week later.

Heterotheca graminifolia (N=18) x H. adenolepis (N=18). Pollen stainability was high in both parents, the latter usually over 90 percent, and the former usually over 97 percent. The F_1 hybrids had pollen stainability

from 48-65 percent with a number of misshapen grains.

The plants tended to be more like H. adenolepis in general appearance as far as size of head, number of flower parts, and size. The peduncles were sometimes glandular like H. adenolepis and in other plants pubescent with a few hidden glands as in H. graminifolia. The anther sac length and stigma papillar length tend to be intermediate between the two species. The pubescence in general was intermediate between the two species in most plants. This would be one of the most difficult hybrids to be able to distinguish in the field and as a result many of the specimens are hard to "fit" in a general key.

Heterotheca ruthii (N=9) x H. pinifolia (N=9). The pollen of the former stained well above 90 percent, and that of the latter species varied from a low of 51.4 percent, but in most cases was above 87 percent. The F_1 hybrid pollen stainability was 67.2 percent. Most of the pollen grains appeared normal.

The general appearance of the hybrid was more like H. pinifolia in shape of the leaves and the more slender aspect. The leaves (2-3 mm wide), while wider than normal H. pinifolia leaves, were still narrower than the leaves of H. ruthii (2.8-5 mm). The pubescence of stem and leaves was intermediate. The peduncles were glandular with small light-colored glands like H. ruthii. The phyllaries had

some glands and appeared intermediate. Phyllary length was 4-6 mm (intermediate).

Heterotheca ruthii (N=9) x H. flexuosa (N=9). The pollen stainability of the former was above 90 percent, and the latter usually above 95 percent. The hybrid plant pollen stainability was 58.9 percent.

These hybrids are more like H. flexuosa in general appearance with the flexuose stem and undulate leaves. The pubescence of stem and leaves was intermediate but not as sericeous as H. ruthii. The peduncles and phyllaries were glandular and tomentose with light-colored glands and hairs. As the head and flower sizes were similar to those in the parents, no difference was noted in the F_1 hybrid plants. Strigose hairs with a bulbous base as is found in H. flexuosa were noted on leaves.

Heterotheca flexuosa (N=9) x H. pinifolia (N=9). The pollen stainability in the former was above 95 percent (except for one count of 67.2 percent) and the latter generally above 87 percent but sometimes as low as 51.4 percent. The F_1 hybrid pollen stainability was 65.0 percent. Most of the pollen grains were regular in shape.

These plants were intermediate in aspect but tended toward H. flexuosa as the leaves were undulate and the stem was somewhat flexuous in appearance. The pubescence was thin on the leaves, but occasional strigose hairs with

bulbous bases as in H. flexuosa were seen on the underside of leaves. The stem was thinly pubescent and purplish (as in H. flexuosa). The peduncles were thinly tomentose with light-colored hairs. The heads and flowers appeared to be intermediate in size.

Heterotheca pinifolia (N=9) x H. falcata (N=9). The achenes produced in this crossing have failed to germinate.

General Ecology

In general almost all of the species in section Pityopsis occur in the Coastal Plain or Piedmont regions. The general habitat of most of the species of section Pityopsis indicated on the labels used the terms: sand or sandy, pine, and dry. The species with habitat preferences differing from these are: H. ruthii which is found only on soil on rocks and in crevices along a river and H. oligantha which is usually found in moist or boggy areas. While the above information agrees with the writer's field observations, the percentages in Table VIII are based upon herbarium specimen labels and reflect the various collectors' observations of habitat. These percentages are based upon the herbarium specimens on loan from various herbaria and range from as few as 20 specimens (H. ruthii) to over 700 (in H. graminifolia and H. microcephala). Of course, a number of herbarium labels contained no habitat information.

TABLE VIII

DATA ON HABITAT OBSERVATIONS AS NOTED ON HERBARIUM LABELS OF SECTION PITYOPSIS (AS PERCENTAGES)[a]

Habitat	Aden (142)	Asp (15)	Fal (86)	Flex (16)	Gram (182)	Micro (156)	Micro Aeq. (23)	Olig (59)	Pin (22)	Ruth (7)
	Number of Labels[b]									
Sand	37	50	70	63	40	46	44	24	73	-
Dry	41	17	16	14	11	13	17	3	-	-
Pine	24	30	27	14	20	34	31	44	-	-
Pine-oak	5	11	-	14	14	3	-	-	5	-
Oak	7	9	-	21	4	3	-	-	5	-
Open (fields, savannahs)	10	9	7	-	16	14	-	5	10	-
Woods	14	-	3	-	10	5	7	13	5	-
Roadside	6	33	7	-	10	5	12	7	21	-
Clay	8	-	-	-	1	1	-	-	-	-
Rocks	5	-	-	-	2	3	-	-	-	100
Wet (boggy)	-	-	-	-	2	4	-	56	-	-
Shale	-	-	-	-	2	-	-	-	-	-
Miscellaneous	1	-	-	1	-	-	-	-	-	-

[a]Percentages may total over 100 as more than one habitat could occur on a label.

[b]Number in parentheses shows labels with habitat observations.

In most cases section Pityopsis plants will be found in open areas (savannahs, roadsides, et cetera) or in open woods whether it is pine, pine-oak, or oak woods.

Apparently all of the species in the section have evolved some specialized structures (Stebbins, 1952) for an arid existence. He includes reduction in leaf surface, development of trichomes (glandular and non-glandular), and others which can be found in all (except H. oligantha) the species in section Pityopsis as adaptations to a dry habitat condition.

CHAPTER V

PHYLOGENETIC CONSIDERATIONS

In Heterotheca section Pityopsis certain phylogenetic speculations can be made with the present data studied. In general the main taxonomic problems have been in the H. graminifolia group. The four species in the H. pinifolia group have been recognized as distinct in the past and are so recognized in this study.

Several clues have been found in this study which will be helpful in determining the phylogeny of section Pityopsis. All the taxa have been cytologically examined and a chromosome number determined. Seven are diploid (N=9), one has both diploid and tetraploid entities (N=9, 18), and two are tetraploids (N=18). Harms (1963) and Pinson (1965) consider the base number to be N=9 in Heterotheca. This compares with Raven, et al., (1960), and Solbrig (1963) who report that the basic number for most Astereae is N=9. While additional hybridization studies are needed, a number have been made in the greenhouse, and one natural hybrid has been found in the field. The author postulates that additional natural hybrids may have been the ancestors of H. adenolepis. Several field studies were made with mass collections in certain localities. Additional morphological

data have been studied for all species.

In using a modified Wagner Ground Plan, Whiffen and Bierner (1972) did not designate which character state was primitive and which was advanced. However, since one taxon must be selected as the most primitive, this essentially selects which character states are thought to be primitive. In all cases, whether a modified Wagner Plan or a regular Wagner Ground Plan (1961) is used, some knowledge is needed of the group under consideration as subjective decisions are needed in both methods.

Characters and character states (Table IX) were chosen to provide differences which would be generally clear cut with few intermediate conditions. An arbitrary judgment was made in using H. aspera as the most primitive. However, it is concluded in this study that H. aspera and H. microcephala var. microcephala are about equally primitive. The main differences between H. adenolepis, H. aspera, and H. microcephala var. microcephala is the degree of glandularity and pubescence on the stem and peduncles. Probably non-glandular one-celled pubescence hairs are more primitive than a simple capitate multicellular gland (Uphof and Hummel, 1962). However, the sericeous pubescence of section Pityopsis is probably more advanced than simple pubescence. In this case both are probably more advanced than a plant with simple one-celled short hairs. Table X

TABLE IX

CHARACTERS AND CHARACTER STATES USED IN SECTION PITYOPSIS

Character	State 0	State 1
1. Stem	Glandular	Pubescent
2. Peduncle	Glandular	Pubescent
3. Phyllaries	Glandular	Pubescent
4. Disc flowers	> 30	< 30
5. Stem height	> 40 cm	< 40 cm
6. Phyllaries	> 50	< 50
7. Bracteoles intergrating with phyllaries	No	Yes
8. Disc corolla tube length	> 6 mm	< 6 mm
9. Ray flowers	> 10	< 10
10. Ligule length	> 7 mm	< 7 mm
11. Involucral height	> 7 mm	< 7 mm
12. Number of heads	> 15	< 15
13. Leaf width/length ratio	> .15	< .15

TABLE X

CHARACTER STATES FOR THE TAXA OF SECTION PITYOPSIS

Taxon	Character State												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Asp	0	0	0	0	1	0	0	0	0	0	0	1	1
Aden	.5	0	0	0	1	0	0	0	0	0	0	1	1
Fal	1	1	1	1	0	1	0	0	1	0	1	1	1
Flex	1	0	1	1	0	1	1	1	1	0	1	1	0
Gram	1	1	.5	1	1	1	.5	1	1	1	1	1	1
Micro	1	1	.5	0	1	0	1	0	.5	0	0	1	1
Micro aeq.	1	1	.5	0	1	.5	1	0	.5	0	1	1	0
Olig	0	0	0	1	1	1	0	1	1	1	1	0	0
Pin	1	1	1	0	0	1	0	0	1	1	0	1	1
Ruth	1	0	0	1	0	1	0	0	1	1	1	0	0

indicates the character states for the taxa, and Table XI tabulates the computed differences between the species. Closely related taxa as seen in Table XI would have a small number difference and distantly related would have a higher number of differences.

A modified Wagner Tree (after Whiffen and Bierner, 1972) is seen in Figure 8. This indicates a close relationship within the H. graminifolia group with only H. oligantha being placed near H. ruthii in the H. pinifolia group. In Figure 9 is seen a different method of analyzing relationships via Paired Affinity Indices (PA) which shows graphically relationships. This method is normally used for chromatogram similarities (Radford, et al., 1972) but was modified using the 13 characters from the modified Wagner Tree computations. It can be seen that four taxa seem closely related (H. adenolepis, H. aspera, H. microcephala--both varieties). With each of the four, affinity is also shown with an arm to H. graminifolia. The four species in the H. pinifolia group appear to have high affinities within the group and also toward H. graminifolia and H. oligantha. Heterotheca falcata and H. flexuosa are closely matched. Heterotheca pinifolia while in general shape matching its group has also a fairly high affinity with every species in the section. In fact, its lowest affinity is with H. flexuosa and the highest with H. falcata

TABLE XI

COMPUTED DIFFERENCES BETWEEN THE TAXA IN SECTION PITYOPSIS

Taxon	Asp	Aden	Fal	Flex	Gram	Micro	Micro Aeq.	Olig	Pin	Ruth
Asp	0	0.5*	8.0	10.0	9.0	4.0	6.5	8.0	7.0	9.0
Aden		0	7.5	9.5	8.5	3.5	6.0	8.5	6.5	8.5
Fal			0	4.0	4.0	6.0	5.5	8.0	3.0	5.0
Flex				0	5.0	8.0	5.5	6.0	7.0	5.0
Gram					0	6.0	5.5	5.0	5.0	6.0
Micro						0	2.5	11.0**	5.0	10.0
Micro aeq.							0	8.5	6.5	7.5
Olig								0	9.0	3.0
Pin									0	6.0
Ruth										0

*Closely related.

**Distantly related.

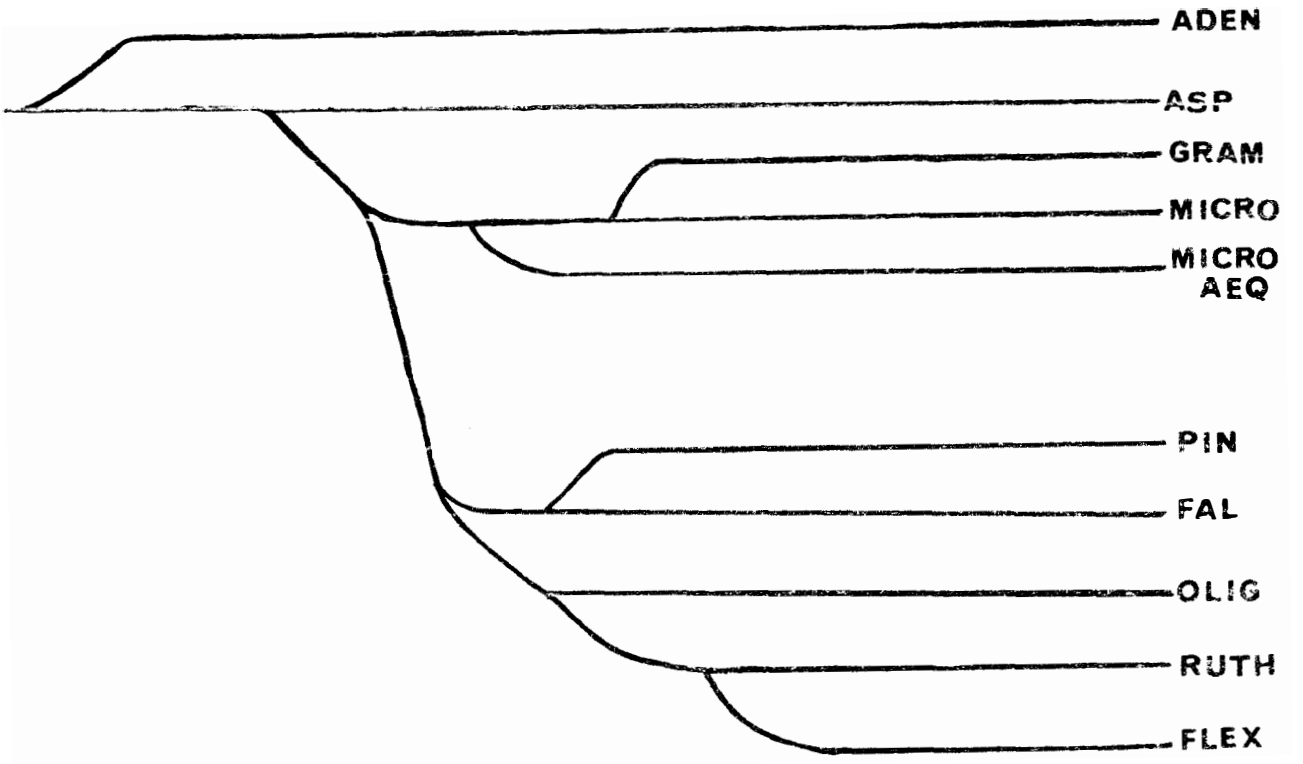

Figure 8. Modified Wagner tree of Heterotheca section Pityopsis.

Figure 9. Paired affinity indices of species in Heterotheca section Pityopsis.* Dots on each arm = 50 percent mark, outer end = 100 percent affinity. Each arm as lettered, represents one taxon, as follows:

A. H. adenolepis.

B. H. aspera.

C. H. falcata.

D. H. flexuosa.

E. H. graminifolia.

F. H. microcephala var. aequilifolia.

G. H. microcephala var. microcephala.

H. H. oligantha.

I. H. pinifolia.

J. H. ruthii.

*Based upon character and state differences and likenesses in Table X, page 60.

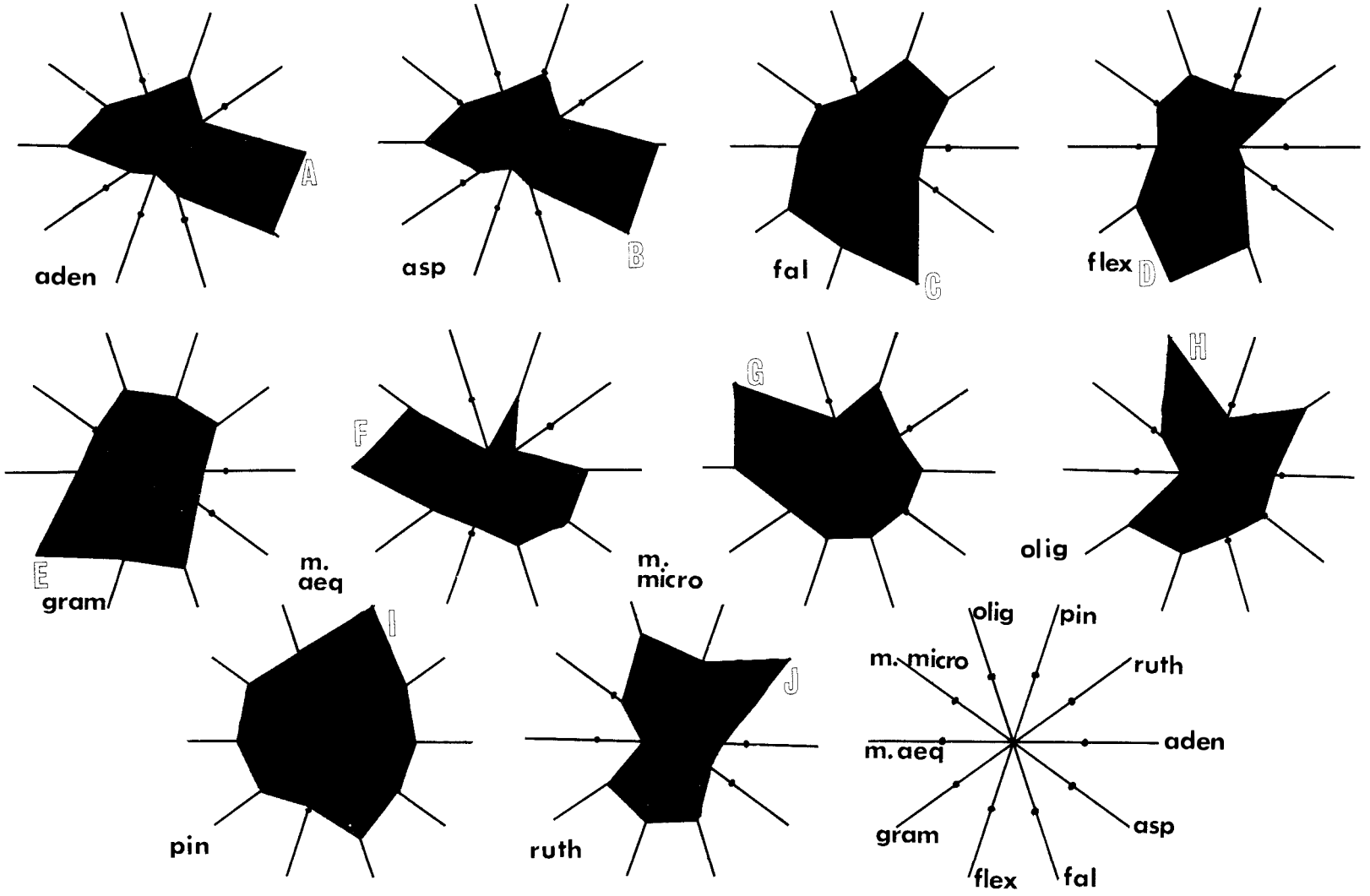
aden
A
asp
B
fal
C
flex
D
E
gram
F
m.
aeq
G
m.
micro
H
olig
I
pin
J
ruth
olig
pin
m. micro
ruth
aden
m. aeq
asp
gram
flex
fal

Figure 9

and then H. ruthii, H. graminifolia, and H. microcephala. Heterotheca ruthii has its highest affinity with the tetraploid H. oligantha, then with others in the H. pinifolia group, and least with H. aspera, H. adenolepis, and H. microcephala var. microcephala. Heterotheca graminifolia appears intermediate between the groups but least related to H. aspera and H. adenolepis. It has generally equal affinities with the other taxa. H. oligantha appears least related to the species, mentioned for H. graminifolia, and its highest affinities with H. ruthii and H. graminifolia.

As it is thought that by the author the whole section Pityopsis is closely related and that has been only through past geographical separation of the entities involved which has kept most of the species genetically and morphologically separated. Further breeding studies are needed to see if sterility barriers occur in areas where species which have the same diploid or tetraploid number occur but apparently do not hybridize such as in Florida, Georgia, and Alabama.

Figure 10 is an attempt to graphically present the author's concept of the phylogeny of section Pityopsis. A primitive ancestor is hypothesized for both H. aspera and H. microcephala var. microcephala, and they are considered equally primitive. It appears that H. adenolepis

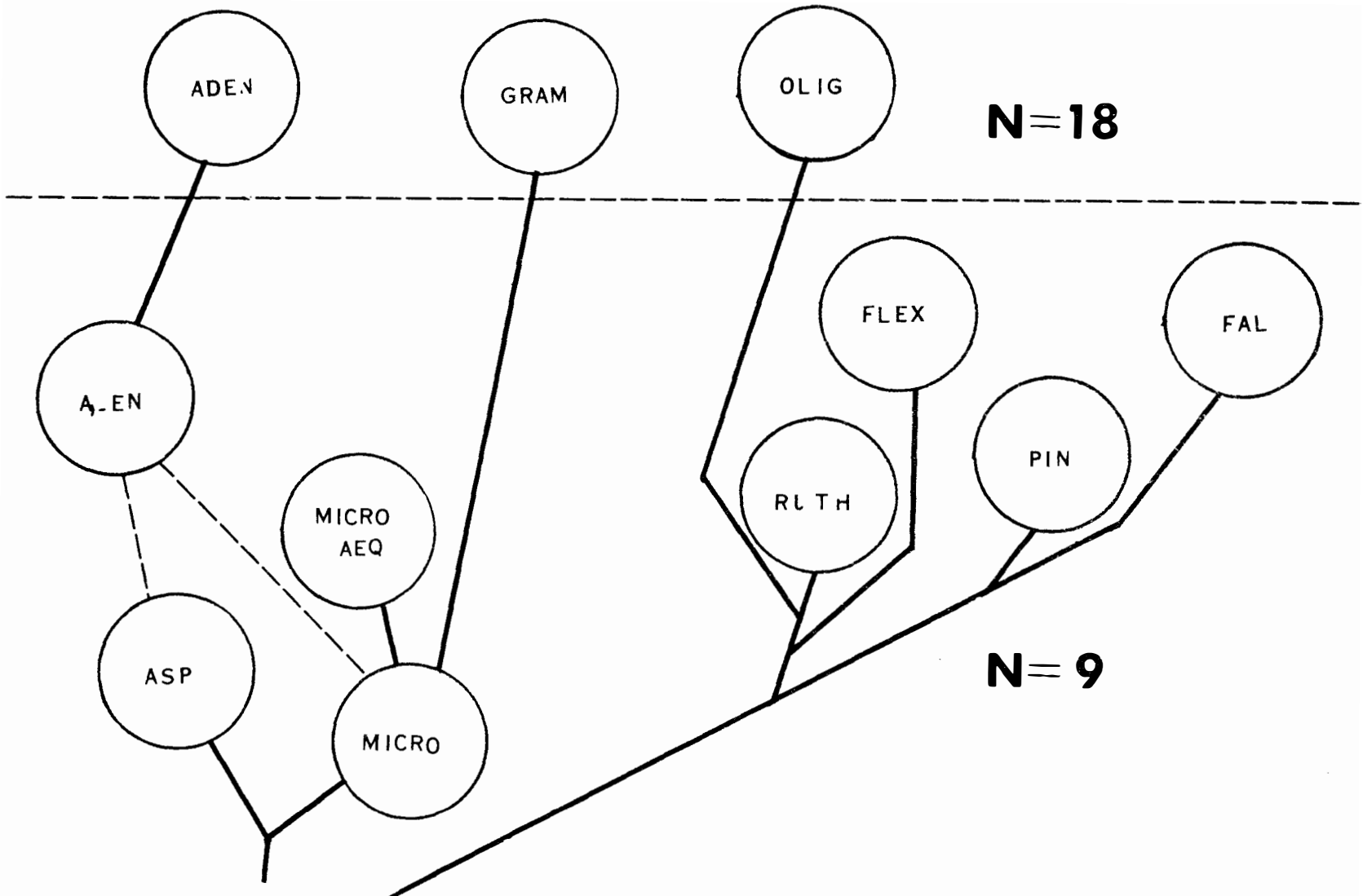

Figure 10. Phylogeny chart of Heterotheca section Pityopsis.

is intermediate between H. aspera and H. microcephala var. microcephala. In Figure 10 speculation is proposed that H. adenolepis (N=9) was formed by hybridization between H. aspera and H. microcephala and then the tetraploid (N=18) was produced through doubling of the chromosomes. One of the difficulties in this speculation is the few numbers and locations of diploid populations of H. adenolepis. However, at some time in the past this diploid probably produced viable offspring allopolyploids which gave rise to the tetraploid H. adenolepis which is apparently well suited to conditions found in the Piedmont region. In Hamilton County, Florida, H. aspera, H. microcephala, and H. adenolepis were growing together. The H. adenolepis plants there resembled diploid plants, but no good cytological material was obtained. Further experimental studies are needed to obtain hybrids between H. aspera and H. microcephala var. microcephala and to produce the allopolyploid artificially.

Heterotheca graminifolia has apparently been derived from H. microcephala var. microcephala through autopolyploidy. H. microcephala var. aequilifolia is postulated to have been derived from the type variety perhaps through geographical separation during the Miocene when Florida existed only as islands such as "Orange Island" (Schuchert, 1935).

It is postulated that H. pinifolia and H. falcata are closely related and were probably derived from a common ancester. Also while closely related to the above two species, H. ruthii and H. flexuosa were also possibly derived from the same or similar primitive ancestor. Since H. ruthii appears to be the most primitive of the four species, it is possible (except for its different ecological niche) that it could have been that primitive entity.

H. oligantha is thought to be closely related to H. ruthii and as a polyploid derivative possibly was derived from it or an ancestor of H. ruthii. It is near the range of H. flexuosa and H. aspera, but does not appear closely related to either one.

The geological sequences which may have occurred to bring about the present distribution of species in this section are important to an understanding of the number of endemics or species with limited range in this section. A number of Heterotheca species occur in the western United States in sections other than Pityopsis. It is thought that the present distribution of section Pityopsis (Figure 11) could have occurred in two ways. One is that it is a western element which migrated eastward during thermal periods in Mid-Pliocene (Duke, 1961) or Oligocene (Axelrod, 1958), and we see the remnants of that migration today. The other is that probably it spread from the West, but at

Figure 11. Distribution map of section Pityopsis (dotted area) and physiographic province map.

Section Pityopsis species.

a *H. adenolepis*.

f *H. flexuosa*.

fa *H. falcata*.

g *H. graminifolia*.

m *H. microcephala* var. *microcephala*.

m *H. microcephala* var. *aequilifolia*.

o *H. oligantha*.

p *H. pinifolia*.

r *H. ruthii*

s *H. aspera*

Physiographic provinces.

1. Coastal Plain.
2. Piedmont.
3. Blue Ridge Province.
4. Valley and Ridge Province.
5. Appalachian (Cumberland) Plateau.

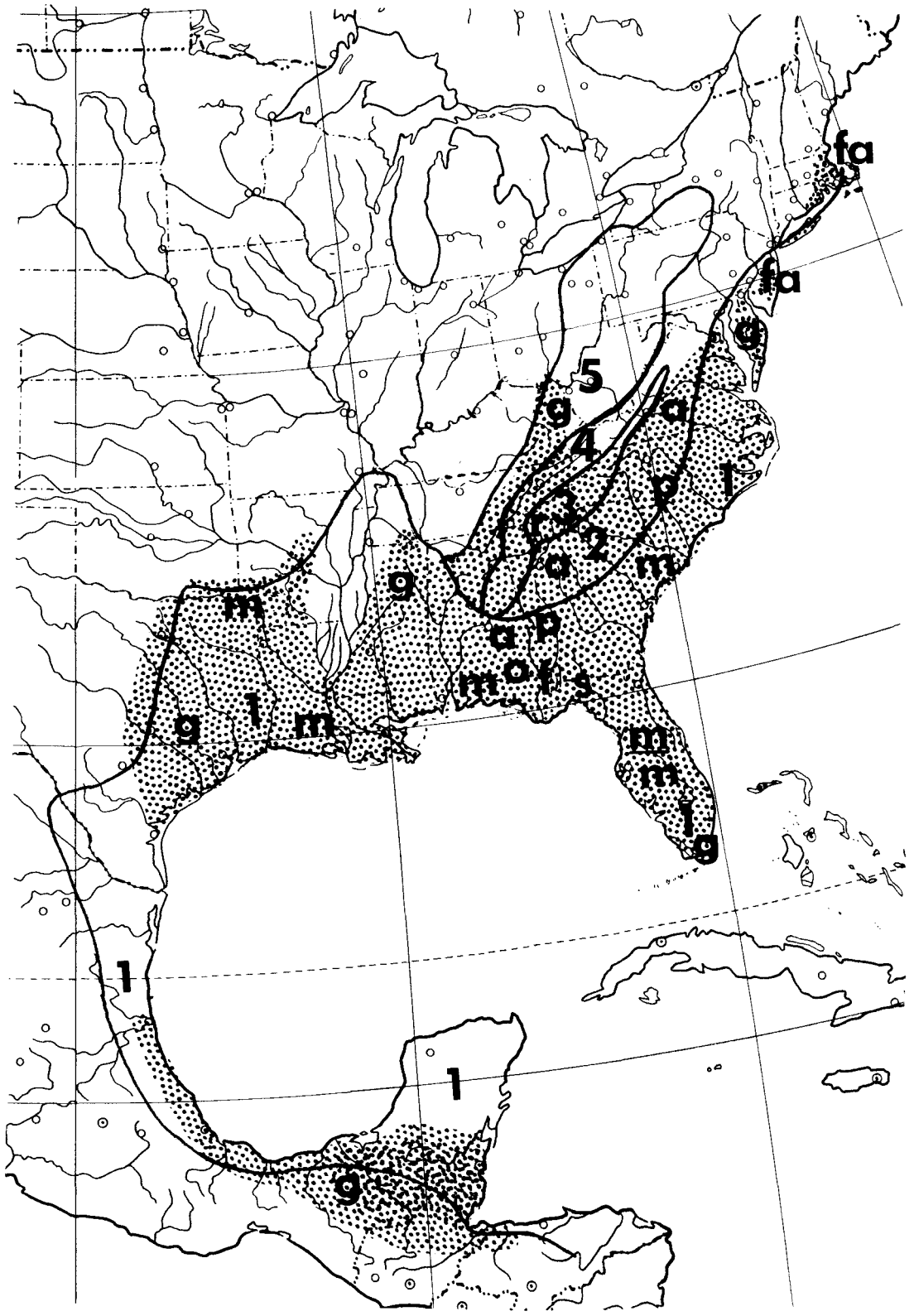

Figure 11

an earlier period, and was at first centered in the Appalachian area and spread from there to occupy its present range today. The author feels that the latter theory is proposed as a logical choice to explain the modern distribution of section Pityopsis.

Only three species still exist in the Appalachian region: H. ruthii (an endemic), H. graminifolia, and H. adenolepis (outer fringes). A collection of F. W. Pennell #20366 (P, DUKE, GA) from Cumberland County, Tennessee in 1935 appears to be H. microcephala var. microcephala, but this is so far removed from the known range of this species, and as no such plants have been found in collecting trips to the same area the accuracy of the locality is in doubt.

These three species may well be the relicts of a once widespread section Pityopsis flora. Other relict species which occur in the Appalachians have produced similar thoughts.

Kearney (1897) wrote:

> Much more probably they are lingering survivals of a more southern flora, once widely distributed over the southern Appalachian region,

and Lucy Braun (1937) said:

> Coastal Plain species of the Cumberland Plateau are relics, and they occupied this area before and during the development of the distinctive Coastal Plain Flora a part of which was then derived from the Appalachian highlands.

It is thought that at least two and possibly all three of the above species listed above are relics from the past. H. ruthii, the very limited endemic, is certainly a relict and possibly barely surviving in a habitat unique for the section. It is possible that it could not compete successfully with other plants in a habitat typical of the other taxa, sandy soil, and thus was forced to survive in a still dry but different habitat, crevices in phyllite rocks. The other relict, H. graminifolia, survived in areas of sandy soil on the Cumberland Plateau and also occurs fairly frequently on shale areas in the Unakas. Heterotheca adenolepis occurs on the fringes of the Appalachians and possibly is a fairly recent invader from the Coastal Plain instead of a relict.

If H. graminifolia is a relict from Post Cretaceous time and is a polyploid derivative of H. microcephala var. microcephala, then the latter must have been present also. H. graminifolia has its northern-most range in southern Ohio (Braun, 1928) as does the southern pine (Pinus echinata) in unglaciated territory. Both H. graminifolia and H. microcephala var. microcephala have similar ranges in the southern Coastal Plain, but H. graminifolia extends further north on the coast to Virginia and Delaware and also north on the Cumberland Plateau to Kentucky and Ohio. This may indicate it can tolerate more diverse climatic

conditions and habitats than H. microcephala which is also widespread. Heterotheca graminifolia in Tennessee, Ohio, and Kentucky is isolated from the main population centers of H. graminifolia and it varies enough in those states to be noticeable (generally smaller flower parts and some glands on peduncle) but not enough to be recognized taxonomically. Thus it is thought that H. microcephala var. microcephala or a form thereof migrated into the Piedmont and, when available, Coastal Plain areas. Heterotheca aspera, if this theory is correct, migrated into the same areas.

Since the Piedmont has been available for plant inhabitation since about the Cretaceous period, H. microcephala var. microcephala and H. aspera could have been the parents of H. adenolepis there. Perhaps with time the two parent species were displaced by the polyploid derivative from that hybrid.

C. W. James (1961) concluded:

> There is no evidence from this study that the relict endemics or disjuncts of northern species in Florida have had a Tertiary origin from a land mass other than Appalachia.

He also indicated that post-Oligocene refugia could have existed in the Marianna Red Hills (near Tallahassee). This would have provided an area for a refuge for H. aspera (and also H. oligantha and H. flexuosa) on the mainland.

It is thought that four species (H. ruthii, H. flexuosa, H. falcata, and H. pinifolia) were derived from

one or two common primitive ancestors. Heterotheca ruthii is thought to be the most primitive species of the four. Migrations may have been from the Appalachian region eastward and southward, eventually finding a suitable habitat (sand?) in possibly the Sand Hills or Red Hills which has been available for plant occupancy since the Cretaceous (Fenneman, 1938). These are weathered remnants of Tuscaloosa sandstone (Duke, 1961). Becoming widespread this ancestral taxon may have then invaded the New Jersey area (Beacon Hill Formation) which has been exposed since Miocene times (Lutz, 1934). Long Island, Cape Cod, and Martha's Vineyard are recent geologic features composed mostly of glacial drift of Pleistocene origin (Fenneman, 1938). As the land receded, the plants became geographically separated. Through evolution of their particular genotypes in response to a changing environment, the remnants of the former primitive ancestor exists today as four species geographically isolated from each other but on the basis of breeding studies not yet genetically isolated.

This compares with what Fernald (1931) postulated had occurred in species like Drosera filiformis (and varieties) and Xyris torta:

> . . . forced . . . to abandon their once congenial but now uncongenial haunts on the Appalachian area and to move out to the newly available xerophytic and

> hydrophytic habitats chiefly on the Coastal Plain . . . where acid savannahs, bogs, shallow pools and dry sands supply the ecological conditions in which these descendants of Cretaceous and early Tertiary hygrophytes and xerophytes can still survive.

As mentioned before, H. microcephala var. aequilifolia is probably derived from the type variety during Oligocene time when central Florida was separated as islands (Schuchert, 1935) which provided an environment for isolating mechanisms to function. Later the area could have been re-invaded by H. microcephala var. microcephala.

Heterotheca oligantha is apparently a polyploid derivative of the primitive ancestor of the H. pinifolia group. Heterotheca ruthii is thought to be the least changed from that primitive ancestor and is also the closest relative of H. oligantha which has become genetically distinct through habitat isolation (moist sand) and its phenology (spring flowering). It probably originated in the Marianna Red Hills of Florida and has spread little since that time.

The spread of H. microcephala var. microcephala and H. graminifolia into the western section of the Coastal Plain probably occurred during the Pleistocene. It may also have been at this time that H. graminifolia invaded the Coastal Plain areas of Mexico, Honduras, and Guatemala as the seas receded (Kay and Colbert, 1965).

In conclusion, it is thought the most primitive

species are H. microcephala var. microcephala, H. aspera, H. ruthii, and H. graminifolia. Probably H. adenolepis was formed after the migration from the Appalachian area. Later or more advanced species or varieties are H. oligantha, H. falcata, H. pinifolia, H. flexuosa, and H. microcephala var. aequilifolia.

CHAPTER VI

TAXONOMIC TREATMENT

Generic Treatment

Heterotheca Cassini, Bull. Sci. Soc. Philom. Paris, s.3, 1817: 137. 1817.

Sideranthus Nutt., in Fras. Cat. 1813. (*Pro parte*: *nomen nudum*).

Diplopappus Cassini, Bull. Sci. Soc. Philom. Paris, s.3, 1817: 137. 1817 (*Nomen illegitimum*).

Diplogon Raf., Am. Monthly Mag. and Crit. Rev., 2: 268. 1818 (*Nomen rejeciendum*).

Inula sect. *Chrysopsis* Nutt., Gen. N. Am. Pl., 2: 150. 1818.

Chrysopsis (Nutt.) Elliott, Sk. Bot. S. C. and Ga., 2: 333. 1824.

Calycium Elliott, Sk. Bot. S. C. and Ga., 2: 339. 1824.

Diplocoma Don in Sweet, Brit. Fl. Gard., 3: 246. 1828.

Stelmanis Raf., Fl. Tellur., 2: 47. 1836.

Hectorea DC., Prodr., 5: 95. 1836.

Chrysopsis sect. *Herbaceae* DC., Prodr., 5: 326. 1836.

Pityopsis Nutt., Trans. Am. Phil. Soc., s.2, 7: 317. 1841.

Ammodia Nutt., Trans. Am. Phil. Soc., s.2, 7: 321. 1841.

Heyfeldera Bip. Schulz, Flora 36: 35. 1853.

Hysterionica Willd., sec. Heterotheca (Cass.) Baillon, Hist. Pl. 8: 155. 1886.

Hysterionica Willd., sec. Chrysopsis (Nutt.) Baillon, Hist. Pl. 8: 155. 1886.

Annual, biennial or rather commonly perennial, herbaceous or sometimes suffrutescent plants. Stems erect or decumbent, simple or branched, with pubescence setose, hirsute, strigose, pilose, villous, lanate, tomentose, sericeous, or glabrous, sometimes with sessile or stipitate glands. Leaves alternate, simple, entire to serrate, either spatulate, obovate, oblong, elliptic, ovate, lanceolate, or linear with pubescence various. Veins in leaves reticulate or parallel-veined. Lower leaves with distinct petiole or attenuate; upper leaves mostly sessile, sometimes clasping. Peduncles leafy-bracted to almost naked with much reduced bracts. Inflorescence determinate, simple, subumbellate, cymose to compound cymose-paniculate. Involucres cylindrical-turbinate, hemispheric, to broadly campanulate. Phyllaries imbricate in several graduated series, 1-nerved, linear, lanceolate

to oblanceolate, scarious to partly herbaceous, appressed to squarrose, pubescence as in stems and leaves. Heads mostly radiate, few discoid. Ray florets seldom lacking, 6-35 in number, pistillate, sometimes abortive, ligules linear to oblong-elliptic, entire to tridentate at apex, tube glabrous to sparsely pubescent, florets with varying shades of yellow; style slender; stigma bifid and lobes linear to narrowly lanceolate, glabrous to puberulent or fimbriate at tips; achenes triangular, cylindrical, fusiform, or obovoid with pubescence hirsute, pilose, puberulent, sericeous, glandular, or glabrous; pappus double or absent (section Heterotheca), outer series of none to many short setose, often lacerate, paleaceous squamellae, inner series of numerous barbellate capillary bristles. Disc florets numerous, perfect, corolla yellow, pubescent to glabrous, narrowly tubular below, widening upward to a campanulate funnelform throat with five acute lanceolate to deltate, somewhat spreading lobes; stamens, five, with short, glabrous to sparsely pubescent filaments, the anthers linear with lanceolate terminal appendages usually exserted beyond lobes during anthesis; style slender, glabrous; stigma bifid with linear flattened to narrowly-lanceolate lobes, puberulent at base to fimbriate or pilose at the tips; achenes cylindrical, obovoid, fusiform, frequently ribbed, also sometimes with glandular-like raised

ribs, also frequently compressed, with pubescence hirsute, sericeous, pilose, puberulent or glabrous; pappus double with the outer series of none to many conspicuous or inconspicuous, sometimes deciduous, short fimbriate-paleaceouse to setose or serrulate appendages, inner series of many elongate barbellate or setose capillary bristles. Receptacle alveolate, naked.

Range: Heterotheca (s. lat.) is native to the temperate North American continent ranging from the Atlantic Coast (as far north as Massachusetts) and as far south as the Florida Keys and Bahamas) westward to the Pacific Coast, inward to southern Ohio, southern Manitoba, Saskatchewan and southern British Columbia, and southward to Baja, California, and the state of Oaxaca, Mexico, Guatemala, and Honduras.

Type species; HETEROTHECA SUBAXILLARIS (Lam.) Britt. and Rusby. Trans. N. Y. Acad. Sci. 7: 10. 1887.
Inula subaxillaris Lam., Encyc. Meth. Bot. 3: 259. 1789.

Key to the Sections of Heterotheca

1. Heads discoid; outer pappus absent or obscure; plants of the Pacific Coast states or Baja, California . . . . . Sect. Ammodia

1. Heads radiate; outer pappus usually evident.
    2. Ray florets without pappus; lower leaves petiolate with upper sessile because of expanding petiole bases. . . . . Sect. Heterotheca
    2. Ray florets with pappus; lower leaves sessile or upper leaves without expanded petiole bases.
        3. Leaves graminiform, 3-5 parallel-nerved, with white, silky-soft, sericeous pubescence (nearly glabrous in H. pinifolia); achenes linear-oblong to fusiform; plants all perennial. . . . . 4. Sect. Pityopsis
        3. Leaves not graminiform or parallel-nerved; pubescence various; achenes obovoid to conical, usually compressed; plants mostly biennial . . . . . .Sect. Chrysopsis

Sectional Treatment

1. Heterotheca section Heterotheca

Heterotheca Cass., Bull. Sci. Soc. Philom, s.3, 1817: 137. 1817.

Calycium Elliott, Sk. Bot. S. C. and Ga. 2: 333. 1824.

Diplocoma Don in Sweet, Brit. Fl. Gard. 3: 246. 1828.

Stelmanis Raf., Fl. Tellur. 2: 47. 1836.

Hysterionica Willd. sect. Heterotheca (Cass.) Baillon, Hist. des Plantes 8: 155. 1886.

Heterotheca Cass. sect. Heterotheca sensu Wagenknecht, Rhodora 62: 61-76, 97-107. 1960.

Range: Southern United States and Mexico (Figure 12).

Type species: Heterotheca subaxillaris (Lam.) Britt. and Rusby, Trans. N. Y. Acad. Sci. 7: 10. 1887.

Inula subaxillaris Lam., Encyc. Meth. Bot. 3: 259. 1789.

2. Heterotheca section Chrysopsis (Nutt.)

Sideranthus Nutt., in Fras. Cat. 1813. (Nomen nudum)

Diplogon Raf., Am. Mo. Mag. and Crit. Rev. 2: 268. 1818.

Inula section Chrysopsis Nutt., Gen. N. Am. Pl. 2: 150. 1818.

Chrysopsis (Nutt.) Elliott, Sk. Bot. S. C. and Ga. 2: 333. 1824.

Hectorea DC., Prodr. 5: 95. 1836.

Chrysopsis subgen. Phyllotheca Nutt., Trans. Am. Phil. Soc. 3. 2, 7: 317. 1841.

Chrysopsis sect. Herbaceae DC., Prodr. 5: 326. 1836.

Chrysopsis sect. Achycaea Torr. and Gray, Fl. N. Am. 2: 256. 1846.

Figure 12. Distributions of Heterotheca sections Ammodia, Chrysopsis, and Heterotheca.

A. Distributions of sect. Ammodia (horizontal lines) and sect. Chrysopsis (vertical lines).

B. Distributions of sect. Heterotheca.

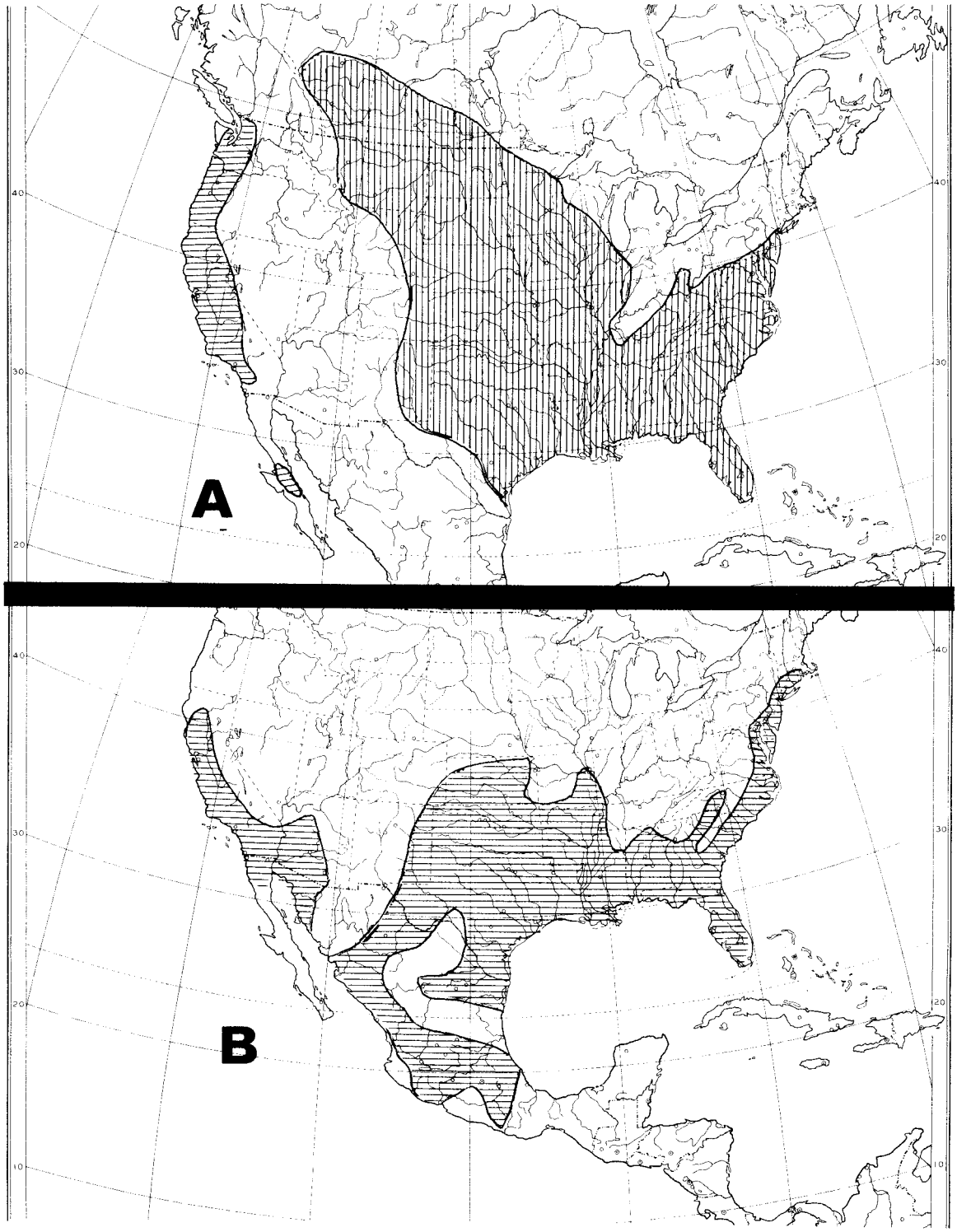

Figure 12

Chrysopsis subgen. Phyllopappus Nutt., Trans. Am. Phil. Soc. 3. 2, 7: 317. 1841.

Range: Southeastern United States westward to the Pacific south to Central Mexico northward to southern Canada and New York (Figure 12, page 85).

Type species: Heterotheca mariana (L.) Shinners, Field and Lab. 19: 66-71. 1951.

Chrysopsis mariana (L.) Ell., Sk. Bot. S. C. and Ga. 2: 355. 1824.

Inula mariana L. (typ. cons. for genus Chrysopsis).

3. Heterotheca section Ammodia (Nutt.)

Ammodia Nutt., Trans. Am. Phil. Soc. 3.2, 7: 321. 1841.

Chrysopsis (Nutt.) Ell. sect. Ammodia (Nutt.) Gray, Proc. Am. Acad. 6: 542-3. 1866.

Chrysopsis subgenus Oreobia Greene, Erythea 2: 106. 1894.

Range: From Washington (mostly west of the Cascades), south through the California Coastal Ranges to Baja, California (Figure 12).

Type species: Heterotheca oregona (Nutt.) Shinners, Field and Lab. 19: 71. 1951.

4. Heterotheca section Pityopsis (Nutt.) Harms, Castanea 34: 402. 1969.

Pityopsis Nutt., Trans. Am. Phil. Soc. 3. 2, 7: 317-318. 1841.

Chrysopsis sect. Pityopsis (Nutt.) Torr. and Gray, Fl. N. Am. 2: 252. 1843.

Heyfeldera Bip. Schulz, Flora 36: 35. 1853.

Perennial herbs; stems simple or branched, ascending or erect, pubescence mostly appressed silky-sericeous sometimes glandular to rarely glabrate; leaves alternate, simple, linear to graminoid, inflorescence cymost-paniculate to corymbiform, involucres tubular to turbinate-campanulate, sericeous to almost floccose (rarely glabrate) sometimes glandular with phyllaries linear to lanceolate, imbricate in 4-12 graduated series; receptacle alveolate, mostly convex, naked; radiate heads; ray florets 8-35, pistillate, ligules various shades of yellow, spreading, linear to oblong-elliptical, entire to tri-entate at apex; disc florets usually numerous, perfect; disc corollas yellow, slender below, tubular then widening above to a funnelform throat with 5 acute lanceolate to deltate spreading lobes; styles slender, glabrous to slightly pilose; stigmas bifid with flattened lobes, puberulent at base to pilose at tips; stamens 5, with short glabrous to slightly pilose filaments, linear anthers bearing lanceolate terminal appendages normally exserted past the lobes at anthesis: pappus double, the outer series of few to many, sometimes deciduous, short

setose-squamellae to fimbriate-squamellate, and the inner series of numerous barbellate capillary bristles; achenes cylindrical to fusiform, usually strongly ribbed, pilose to sericeous.

Range: Chiefly Southeastern United States, northward to Massachusetts, Ohio, and central Arkansas, west to Texas and southeastern Oklahoma, present also as a disjunct in Bahamas, British Honduras, Guatemala, and southern Mexico.

Type species: Heterotheca pinifolia (Ell.) Ahles. J. Elisha Mitch. Sci. Soc. 80: 173. 1964.
Chrysopsis pinifolia Elliott Sk. Bot. S. C. and Ga. 2: 335. 1824.

Key to the Species of Section Pityopsis

1. Basal leaves (when present) greatly exceeding the cauline leaves, at least lower leaves sericeous and graminiform, cauline leaves reduced upward (except in H. microcephala var. aequilifolius) . . . . . .
    2. Inflorescence branches, peduncles, and stems without glands, phyllaries may or may not be glandular, cauline leaves more than 10 . . . . . .
        3. Number of disc flowers less than 30, disc flowers less than 7 mm long, ligule generally

less than 7 mm long, involucral height less than 8 mm. . . . . .

4. Cauline leaves width/length ratio .20 or more, more or less equal upward from base; basal caudex woody, rhizomes absent; peninsular Florida.4. H. microcephala var. aequilifolius

4. Cauline leaves width/length ratio .20 or less, reduced upward on stem; basal caudex not woody, rhizomes usually present; Coastal Plains from Florida northward to southern North Carolina and west to Arkansas and Louisiana . . . . 3. H. microcephala var. microcephala

3. Number of disc flowers greater than 30, disc flowers more than 7 mm long; ligules more than 7 mm long, involucral height more than 8 mm; widespread from Florida northward to Virginia, Delaware, Ohio, west to Arkansas, southeastern Oklahoma, and eastern Texas, disjunctly found in Bahamas, northern Guatemala, and southern Mexico . . . . . 5. H. graminifolia

2. Inflorescence branches, peduncles, and stems glandular, phyllaries glandular, cauline leaves usually less than 10. . . . . .

5. Cauline leaves few; heads fewer than 10, large; involucral height usually exceeding 8 mm; ligule

usually longer than 1 cm and more than 10 in number; plants limited to the panhandle of Florida, Mobile County, Alabama, and southern Georgia . . . . . .7. *H. oligantha*

5. Cauline leaves numerous; heads more than 10, small; involucral height less than 8 mm; ligule less than 1 cm long and less than 10 in number.
   6. Leaves with glandular edge, upper cauline leaves glabrate, lower leaves glabrate above; stem glandular almost to base. Limited to north central Florida and southern Georgia. . . . . 1. *H. aspera*
   6. Only uppermost leaves or bracteoles with glandular edge, leaves usually sericeous; peduncles, and phyllaries glandular; widespread from Virginia south to Florida (especially in Piedmont) west to Louisiana . . . . . 2. *H. adenolepis*

1. Cauline leaves exceeding basal leaves, usually less than 5 mm wide. All below the inflorescence almost equal in length, pubescence various. . . . . .
   7. Peduncles and involucres copiously glandular; leaves sericeous; restricted to Hiwassee Gorge, Polk County, Tennessee . . . . . 8. *H. ruthii*

7. Involucles and peduncles non-glandular (inconspicuously or hidden in H. flexuosa); leaves various. . . 8

8. Involucral height over 8 mm, equalling pappus; stem flexuous; endemic to 4 counties around Tallahassee, Florida . . . . . 9. H. flexuosa

8. Involucral height less than 8 mm, less than length of the pappus; stem not conspicuously flexuous . . . . . .

9. Cauline leaves usually falcate, 2-5 mm wide, pubescent at least along edge of leaf; disc flowers more than 30; limited to Atlantic Coastal Plain from New Hampshire to New Jersey . . . . . .8. H. falcata

9. Cauline leaves crowded, linear-filiform, 5-2 mm wide, almost glabrous; disc flowers less than 30; endemic limited to sandhills of Georgia to central North Carolina. . . . . 10. H. pinifolia

Species Treatment

1. Heterotheca aspera (Shuttlew.) Shinners, Sida 3: 348. 1969.

Chrysopsis aspera Shuttleworth, Bot. Zeit. 3: 221. 1845. (Nomen nudum).

Chrysopsis aspera Shuttlew. ex Gray, Syn. Fl. 1: 121. 1884 (in synon).

C. graminifolia var. aspera (Shuttlew.) Gray, Ibid.

C. aspera Shuttlew. ex Small, Fl. S. E. U. S. 1182. 1903.

Pityopsis aspera (Shuttlew.) Small, Man. S. E. Fl., 1341. 1933.

C. graminifolia sensu Fernald (in part), Rhodora 44: 471. 1942.

Herbaceous rhizomatous perennial; stems erect (usually one), slender, to 5 dm high, but usually shorter, pubescence sericeous lower one-third, upper two-thirds of stem viscid glandular. Basal leaves sericeous glabrate, leaf edge glandular, to 18 (25) cm long and 5-10 mm wide, ascending to spreading, normally forming a loose rosette at base of stem, overwintering. Lower and upper cauline leaves similar to basal leaves but reduced rapidly upward, from 3-8 mm wide and 3-10 cm long to 1-2 mm wide and 2-5 cm long, usually glabrate with glandular leaf edge; peduncular bracts small, glandular, and subulate. Inflorescence ascending-spreading with a few to 100 or more heads, slender peduncles usually 5 mm wide and 1-6 cm in length, covered with viscid stalked glands. Heads small, turbinate, 4.5-7 mm high, 4-5 mm wide, shorter than mature pappus. Phyllaries imbricate in 4-7 series, scarious margined, herbaceous and glandular central portion, ciliate margin, acuminate-lanceolate to 5 mm long. Disc corollas 4-5 mm

long, slightly pilose lobes 0.5 mm long. Ligulate corollas 6-10, ligules 4-5 mm long, and 1.5 mm wide. Pappus double; outer of 15-27 setiform squamellae to 1.0 mm long, inner of barbellate capillary bristles to 5.5 mm long. Achenes fusiform, linear ribbed, to 3.0 mm long, sericeous. N=9.

Flowering time: Usually August to October with other flowering times possible due to injury to the plant.

Type: Rugel s.n., in pinetis inter Tallahassee at St. Marks, Florida, August, 1843. (NY!) (Figure 13).

Variation and ecology: Heterotheca aspera has been rarely collected--only a few (30) specimens were seen and two sample areas collected. It is necessary to limit the name, H. aspera, to this restricted taxon. The type is very characteristic of the collections named: H. aspera by the author, which have glandular-edged leaves, stem glandular almost to the base, and leaves almost glabrate except for glands. Heterotheca aspera is a diploid (N=9). No meiotic irregularities were found.

This name, H. aspera, was in the past used for all plants which were glandular on the stem, and peduncle, and with small heads. This study separates these plants into two entities--H. aspera and H. adenolepis. This is further discussed under H. adenolepis.

Probably only H. adenolepis or H. microcephala could be mistaken for H. aspera. However, it is clearly separated

Figure 13. Type specimen of Heterotheca aspera (Shuttlew.) Shinners.

using characters in Table XII. Further study is needed on this species and possible hybrids between it and H. microcephala and H. adenolepis. No hybridization attempts were successful (as of now) in the greenhouse. The data in Table VIII, page 56, indicates again sand, pine, dry, and also roadsides for this taxon. This range again is an area of endemics (see H. flexuosa) around Tallahassee, Florida, except it extends to near the Sewanee River. The forest region would be oak-hickory-pine and fine to coarse sand-loamy soils.*

Distribution: A rather limited distribution in the northern area of Florida involving only counties all north and west of the Sewanee River (Figure 14b).

Representative specimens: A total of 30 herbarium specimens of this taxa were studied, plus two population samples. The following are all those studied: FLORIDA: Hamilton Co., Bowers and Wofford #71-561 (TENN); Jefferson Co., Godfrey #70124 (FSU); Leon Co., Godfrey #54304 (FSU, GH, NY), Bowers #45590 (TENN); Liberty Co., Wiegand and Manning #3188 (CU); Sewanee Co., Curtiss #6939 (MO, US, GH, GA, NY), Curtiss #10967E (US); Union Co., Godfrey and

---

*Where soil types are cited the old soil types will generally be listed but under the new classifications; Podzolic and Red-yellow Podzolic would be in the main Ultisols (Nelson and Zillgitt, 1969). The new soil type name will be listed in parenthesis with the old when determinable. The major forest types are from Küchler (1970).

TABLE XII

DIFFERENCES BETWEEN HETEROTHECA ADENOLEPIS, H. ASPERA, AND H. MICROCEPHALA VAR. MICROCEPHALA

Characters	H. adenolepis	H. aspera	H. microcephala var. microcephala
Upper stem	Pubescent	Glandular	Pubescent
Leaf edge	Non-glandular (occasionally glandular on bracteoles)	Glandular	Non-glandular
Upper leaf pubescence	Sericeous	Mostly glabrate	Sericeous
Peduncle	Glandular	Glandular	Pubescent
Bracteole number	2-5 (usually)	4-7	5-8
Outer phyllary width	0.4-0.8 mm	0.6-0.9 mm	0.3-0.7 mm
Ligule length	4-5.4 mm	4-5 mm	4.2-7 mm
Disc corolla tube length	4.5-6 mm	4-5 mm	4-6.5 mm

Figure 14. Distribution of Heterotheca adenolepis and H. aspera.

A. Distribution of H. adenolepis.

B. Distribution of H. aspera.


MINNESOTA
WISCONSIN
IOWA
ILLINOIS
INDIANA
OHIO
MISSOURI
KENTUCKY
TENNESSEE
ARKANSAS
MISSISSIPPI
ALABAMA
GEORGIA
LOUISIANA
NEW YORK
PENNSYLVANIA
MAINE
A
B

Figure 14

Morrill #52548 (DUKE, FSU).

GEORGIA: Brooks Co., Harper #1619 (F, MO, GH, US, NY); Decatur Co., Godfrey #69010 (FSU); Lowndes Co., Quarterman #118 (DUKE), Quarterman #411 (DUKE), Quarterman #468 (DUKE).

2. Heterotheca adenolepis (Fern) Ahles. J. Elisha Mit. Sci. Soc. 80: 172-173. 1964.

Chrysopsis adenolepis Fern., Rhodora 44: 471. 1942.

Chrysopsis graminifolia sensu (in part) Fernald, Rhodora 44: 468. 1942.

Herbaceous usually rhizomatous perennial; stems erect, usually slender, to 6 dm high, usually shorter, pubescent (sericeous) to inflorescence branches, not usually sticky-to-touch. Lower leaves sericeous occasionally shedding hairs, appearing glabrate, leaf edge not glandular, to 30(35) cm long and 2-10 mm wide, ascending to spreading, normally forming a loose rosette base of leaves, over-wintering. Lower and upper cauline leaves usually similar to basal leaves but reduced rapidly upward from 2-8 mm wide and 2-12 cm long to 1-2 mm wide and 2-5 cm long, usually sericeous with no glands along edge of leaf; peduncular bracts small, glandular, and subulate, may appear glandular along edge. Inflorescence ascending-spreading with a few to 100 or more heads, slender peduncles usually 4-8 mm wide and 1-5 cm in length, covered with dark viscid stalked glands.

Heads small cylindric-turbinate to turbinate, 4.5-5.5 mm wide and 4.5-7 mm high, shorter than mature pappus. Phyllaries imbricate in 4-7 series, scarious margined, herbaceous and glandular central portion, ciliate margin, acuminate-lanceolate to 6 mm long. Disc corollas 4-5.5 mm long, slightly pilose, lobes 0.5-0.6 long. Ligulate corollas 6-10 in number, ligules 4-5.5 mm long and to 2.0 mm wide. Pappus double; outer of 15-27 setiform squamellae to 1.2 mm long, outer of barbellate capillary bristle to 5.5 mm long. Achenes fusiform, linear ribbed to 3 mm long, sericeous. N=9.

Flowering time: Usually August to October with other flowering times found due to injury to the plant.

Type: Katzenstein s.n., old barren fields, Pinehurst, Moore County, North Carolina, August 19, 1897. (GH!) (Figure 15).

Variation and ecology: This is the only species with two chromosome levels, N=9 and N=18. Only two counts of N=9 were found. One was made by Jones (#3502) in Mississippi and the other by Bowers (#70-109) in North Carolina. The latter count was made at an area of hybridization between H. pinifolia (N=9) and H. adenolepis (N=9) and is discussed further under H. pinifolia. One other collection from Hamilton County, Florida, is suspected to be the diploid but a meiotic count was not accomplished.

Figure 15. Type specimen of Heterotheca adenolepis (Fern.) Ahles.

Other herbarium specimens were seen which possibly could be the diploid and all were in the southern Coastal Plain region south of North Carolina. It is difficult to separate the two diploids from the tetraploid plants. The diploids appear generally somewhat shorter in stature with less branching. Also, in pollen size (Figure 3, page 36), there is not a significant difference (at the .05 level) near pollen sizes 18.82 to 20.17 μ. Apparently the diploid plants in this species are less frequent than the tetraploid as a number of counts were made of the tetraploid (Table III, page 24), sampled over a wide portion of its range but only two diploids.

The main characters common to the diploid and tetraploid H. adenolepis are:

1. Stem usually pubescent, no visible glands.
2. Peduncles glandular.
3. Small heads and flower parts.
4. Bracteoles usually not integrating with phyllaries.
5. Usually a "greener" appearance of the flower and peduncles.

The other species which could be confused with H. adenolepis are H. aspera, H. graminifolia (in Virginia and North and South Carolina) and perhaps H. microcephala var. microcephala.

The main differences between H. adenolepis and H. aspera are seen in Table XII, page 97. As H. aspera is apparently limited to Florida and Georgia, separation would be most difficult in that area. Heterotheca aspera was the first described species, and other authors have included under its name everything with glandular peduncles (except H. oligantha). Heterotheca adenolepis was described by Fernald (1942) for a plant bearing stolons which he thought were absent in H. aspera (when he then called H. graminifolia, as discussed in the taxonomic section). However, most (if not all) of the many field samples or complete herbarium specimens have at least a short rhizome in all the species of section Pityopsis except H. microcephala var. aequilifolia.

Most of the confusion between H. adenolepis and H. microcephala would be in areas where H. aspera and H. microcephala would hybridize to form a plant like H. adenolepis. This is a possibility in one sample area in Florida where all three species were collected. (This is discussed further in the section on Phylogeny.) In most cases the lack of glands on the peduncle, heavily pubescent phyllaries, and bracteoles integrating with phyllaries would separate H. microcephala from H. adenolepis.

The confusion which exists between H. graminifolia and H. adenolepis apparently is where introgression is

taking place in Virginia and in North and South Carolina where the two species grow together. However, little of this introgression is seen in other areas even where the species may grow together. Whether this is some type of sterility barrier present in the area of non-introgression is not known. The hybridization which was successful in the greenhouse study was between plants from widely separated areas--Tennessee and southern Georgia. These hybrids are intermediate between the two parents. The main differences are noted in Table XIII for H. adenolepis and H. graminifolia. In the great majority of cases, this will differentiate between the two. Also pollen size would be an indication (Figure 3, page 24) of the correct species. Hybrids have a fairly low pollen viability and many misshapened grains. Other morphological factors are that anther sacs in H. adenolepis are usually below 2.25 mm long and H. graminifolia is 2.5 mm or longer; also papillae surface length on the stigma is below 600 μ and the latter above 650 μ in length. Another source of some concern but only in a few instances is the presence of H. graminifolia in Tennessee, Kentucky, and Ohio, well separated from the main body of H. graminifolia. These plants sometimes have glands on the peduncle which normally are hidden by pubescence, but late in the year would be exposed giving a H. adenolepis-like peduncle. They are

TABLE XIII

DIFFERENCES BETWEEN *HETEROTHECA ADENOLEPIS*, *H. GRAMINIFOLIA*, AND *H. MICROCEPHALA* VAR. *MICROCEPHALA*

Characters	*H. adenolepis*	*H. graminifolia*	*H. microcephala* var. *microcephala*
Peduncle	Glandular	Usually pubescent if glandular hidden by pubescence	Pubescent
Phyllary glands	Many	Few to none	Many
Involucral height	5-7.5 mm	8-13 mm	5-8 mm
Ligule length	4-5.4 mm	8-14 mm	4.2-7 mm
Disc corolla tube length	4.5-6 mm	6.5-8.8 mm	4-6.5 mm

also somewhat intermediate between H. adenolepis and H. graminifolia in the characters of anther sac length and papillae surface length on the stigma. However, pollen size is like that of H. graminifolia. Generally most of the characters in Table XIII, page 106, also will separate the two.

Heterotheca adenolepis is primarily a Piedmont and mid-southern (Georgia, Florida, Alabama, and Mississippi) Coastal Plain species (Figure 14, page 98). It is occasionally in the Blue Ridge Province. The data in Table VIII, page 56, indicates habitats of dry (41 percent), sand (37 percent), pine (24 percent) and is also fairly high in clay (8 percent) and rocks (5 percent). In the Piedmont there is a mosaic of soil types (Oosting, 1942). The sedimentary rocks have been weathered to sandy loams with clay subsoils. In the higher elevations of North Carolina and Virginia, where it is found, the habitat is mostly roadside or rocky bluff areas. The areas where this taxon exists would mainly be Oak-Hickory Pine Forests in the Piedmont and longleaf-slash Southern Mixed Forest in the Coastal Plain regions. In the southern regions of the Coastal Plain, H. adenolepis may occur with H. graminifolia, H. pinifolia, H. microcephala, H. aspera, and H. flexuosa. In the sand hill regions of the Piedmont, it may occur with H. pinifolia and H. graminifolia.

Distribution: A rather wide distribution from Florida northward to Virginia, in the Piedmont areas in the Carolinas, west to Mississippi.

Representative specimens: A total 675 herbarium specimens of this taxa were studied along with field collections: ALABAMA: Autauga Co., Harper #3265 (GH, F, NY, MO, US); Baldwin Co., Tracy #8022 (MO, GA, US, F, NY, TEX); Barbour Co., McDaniel #6966 (FSU, VDB); Bibb Co., Jones and Jones #1671 (GA); Bullock Co., s. coll. #10967C (US); Cherokee Co., Kral #33374 (VDB); Clark Co., Kral #29579 (VDB); Covington Co., Shinners #27452 (SMU); Cunecuh Co., Blake #9067 (DUKE); Elmore Co., Justice #460 (CU); Escambia Co., Kral #33875 (VDB); Geneva Co., Kral #33791 (VDB); Houston Co., Wiegand and Manning #3190 (GH, CU); Lee Co., Koelling #2043 (TENN, NCU); Macon Co., Wiegand and Manning #3191 (GH, F); Mobile Co., Pennell #4490 (MICH, NY); Washington Co., Shinners #29037 (SMU).

FLORIDA: Calhoun Co., Godfrey #58839 (FSU); Escambia Co., Shinners #28916 (SMU, FSU); Gadsden Co., Godfrey #55228 (FSU); Gulf Co., Wooten #189 (FSU); Jackson Co., Mitchell #931 (FSU); Leon Co., Godfrey #55219 (GA, FSU, USF); Liberty Co., Redfearn #893-134-55 (FSU); Madison Co., Kral #6173a (FSU); Santa Rosa Co., Godfrey #59050 (FSU); Suwanee Co., Hitchcock #902 (F); Wakulla Co., Godfrey #70073 (FSU); Walton Co., Hood #2906 (KANU).

GEORGIA: Bacon Co., McKay s.n. (GA); Baker Co., Thorne #4388 (GA, CU); Banks Co., Hollingsworth #51242 (GA, NCU); Barton Co., Duncan #8890 (GA, KANU, SMU, MO); Calhoun Co., Thorne #4585 (CU); Clarke Co., Demaree #51211 (NCU, SMU); Columbia Co., Duncan #12038 (GA, DUKE); Decatur Co., Thorne #4440 (CU); Dougherty Co., Duncan #6671 (GA); Elbert Co., Duncan #10567 (GA, MO); Emanuel Co., Wilbur #2922 (GA); Floyd Co., Lipps s.n. (TENN); Fulton Co., Schallert #623 (KANU); Grady Co., Godfrey #69108 (FSU); Gwinnett Co., Small s.n. (PH, F); Habersham Co., Duncan #1229 (GA); Hall Co., Beade #E8396 (GA); Hancock Co., Godfrey #50788 (NY, DUKE); Houston Co., Ainsworth #44917, 12 (PH); Jefferson Co., Hopkins (Herb.) #45 (NY); Johnson Co., Bozeman and Logue #10745 (NCU); Lamar Co., Hamlin #E8043 (GA); Laurens Co., Cronquist #4864 (GA, GH, US, PH, MICH, SMU, NY); Lincoln Co., Pyron and McVaugh #122 (GA); Lumpkin Co., Rogers #42198 (TENN); Marion Co., Duncan #4159 (GA); Miller Co., Thorne #5882 (CU); Muscogu Co., s. coll. #10967d (PH, US); Oglethorpe Co., Fitzgerald #383 (GA); Rockdale Co., Pyron and McFaugh #1109 (GA); Rabun Co., Whitney, Jr., s.n. (GA); Richmond Co., s. coll. s.n. (GH); Rockdale Co., Cronquist #4847 (NY); Sumpter Co., Duncan #1677 (GA, NU); Taylor Co., Dress and Moran #2408 (FSU); Terrell Co., Duncan #1767 (US); Thomas Co., Godfrey #67407 (FSU); Tift Co.,

Shepherd #199 (GA); Upson Co., Cronquist #4697 (GA, GH, MO, SMU, NY); Warren Co., Godfrey #50785 (GA, DUKE, NY); Wheeler Co., Godfrey #50808 (PH, DUKE, GH, NY).

MISSISSIPPI: Clarke Co., Jones and Jones #15259 (GA); Forest Co., Jones #2574 (FSU); Harrison Co., Demaree #32396 (NCU); Jackson Co., Earle and Seymour #91821 (DUKE); Jefferson Davis Co., Jones #14284 (GA, SMU); Lamar Co., Jones, Jr. #3456 (FSU); Stone Co., Jones #10393 (NCU, GA); Wayne Co., Shinners #29063 (SMU).

NORTH CAROLINA: Alamace Co., Ramseur and Hammond #2284 (NCU); Alexander Co., Godfrey and Fox #48647 (FSU); Anson Co., Ahles and Leisner #19434 (NCU); Brunswick Co., Godfrey #49698 (TENN); Burke Co., Wilbur #4937 (GH); Cabarrus Co., Leisner #19608 (NCU); Caldwell Co., Radford #15078 (NCU); Caswell Co., Wilbur #4254 (GA, GH); Catawba Co., Bell s.n. (NCU); Chatham Co., Godfrey and Fox #50025 (F, DUKE); Cleveland Co., Leisner #19145 (NCU); Cumberland Co., Duke #1745 (GH); Davidson Co., Ahles and Leisner #18655 (NCU); Durham Co., Musgrove s.n. (KANU); Forsyth Co., Correll #255 (NCU); Franklin Co., Ahles and Leisner #20559 (NCU); Gaston Co., Fox and Godfrey #5425 (FSU, SMU); Granville Co., Godfrey #5533 (GH); Guilford Co., Bell #14425 (SMU, NCU); Halifax Co., Ahles and Leisner #20690 (NCU); Harnett Co., Fox and Godfrey #50517 (DUKE, GH, TENN, KANU, NY); Henderson Co., Correll #3345 (DUKE);

Hoke Co., Godfrey and Fox #50546 (DUKE, US, NY, GH); Iredell Co., Godfrey and Fox #50291 (DUKE, MO, GH); Johnston Co., Godfrey and Fox #48695 (SMU); Lee Co., Kessler #502 (NCU); Lincoln Co., Bell #15296 (NCU); McDowell Co., Beaman #187 (TENN, DUKE, FSU, KANU, MO, NY, SMU, NCU, GA, GH); Mecklenburg Co., Ahles and Duke #48492 (NCU); Montgomery Co., Radford #19571 (NCU); Moore Co., Godfrey #50114 (NCU, KANU, US, TENN, NY, SMU); Nash Co., Godfrey #5430 (US, GH); Orange Co., H. L. B. #5120 (DUKE); Polk Co., Peattie #2382 (NCU); Randolph Co., Bell #14163 (NCU); Richland Co., Ahles #2245 (NCU); Richmond Co., Godfrey and Fox #50594 (DUKE); Rockingham Co., Oosting #33413 (DUKE); Rowan Co., Heller s.n. (F); Rutherford Co., Fox #5274 (DUKE, FSU, GH, SMU); Scotland Co., Leisner and Ahles #32727 (NCU); Stanley Co., Small s.n. (MO, US, F); Stokes Co., Godfrey and Fox #48581 (SMU); Surry Co., Correll and Correll #14516 (DUKE); Transylvania Co., Freeman #58327 (NCU); Union Co., Ahles #33884 (NCU); Vance Co., Ahles and Leisner #20374 (NCU); Wake Co., Godfrey #48527 (GA, FSU, KANU, SMU); Warren Co., Seaman #3339 (NCU); Yadkin Co., Radford #15440 (NCU).

SOUTH CAROLINA: Abbeville Co., Radford #30824 (NCU); Aiken Co., Smith s.n. (PH, NY); Allendale Co., Bell #5120 (SLU); Anderson Co., Davis (Herb.) #280 (TEX); Bamberg Co., Ahles #37528 (NCU); Barnwell Co., Ahles and

Crutchfield #55724 (NCU); Charleston Co., Godfrey and Boyce #50482 (DUKE, NY); Cherokee Co., Ahles #34217 (NCU); Chester Co., Bell #10063 (NCU); Chesterfield Co., Duke #1412 (NY); Darlington Co., Smith #538 (NCU); Edgefield Co., Radford #30178 (NCU); Fairfield Co., Bell #9909 (NCU); Florence Co., Bell #13447 (NCU); Georgetown Co., Godfrey #50910 (DUKE, NY); Greenville Co., Smith s.n. (GH); Jasper Co., Bell #18074 (NCU); Kershaw Co., Radford #27695 (NCU); Lancaster Co., Huntley #164 (DUKE); Laurens Co., Bell #10205 (NCU); Lee Co., Radford #27380 (NCU); Lexington Co., Godfrey #50779 (GH, DUKE, NY); Marlboro Co., Radford #19043 (NCU); McCormick Co., Radford #30546 (NCU); Oconee Co., House #2905 (US, NY); Orangeburg Co., Leisner and Ahles #31763 (NCU); Pickens Co., Rodgers #225 (DUKE); Richland Co., Rhoads s.n. (SMU); Saluda Co., Radford #26801 (NCU); Spartanburg Co., Bell #10357 (NCU); Sumpter Co., Radford #29649 (NCU); Union Co., Freeman #56630 (NCU); York Co., Ahles #34469 (NCU).

VIRGINIA: Brunswick Co., Kral #9436 (FSU, NCU); Buckingham Co., Baldwin, Jr. #5409 (GH); Charlotte Co., Ahles and James #60833 (NCU); Caroline Co., Fernald and Long #9174 (GH); Chesterfield Co., Smith and Hodgdon #989 (TEX, GH, US, NCU, F, DUKE, GA, MO, MICH, SMU); Dunwiddie Co., Harvill #21026 (NCU); Gloucester Co., Wherry and

Pennell #12728 (F, GA, MO, PH); Greenville Co., Meyncke s.n. (US); Halifax Co., Ramsey and Ramsey and Ruska and Waggoner #8953 (NCU); Hanover Co., s. coll.s.n. (SMU); Henrico Co., Wherry and Pennell #12476 (F, GA, MO, MICH); James City Co., Menzel #119 (MICH, GH); Lancaster Co., Allard #21744 (CU); Lunenburg Co., Ahles and James #61864 (NCU); Middlesex Co., Hermann #10425 (MO); Nottoway Co., Ramsey, Hooks, Baxter #11055 (SMU); Pittsylvania Co., Wherry and Pennell #14365b (DUKE, F, MO); Prince Ed. Co., Ahles and James #62901 (NCU); Prince George Co., Fernald and Long #6711 (US, DUKE, F, MO, GH); Sussex Co., Wilkens #11247 (NCU); Wright Co., Rhoades s.n. (SMU).

3. Heterotheca microcephala (Small) Shinners, Field and Lab. 19: 68. 1951.

Chrysopsis microcephala Small, Fl. S.E. U.S. 1182. 1903.

Pityopsis microcephala (Small) Small, Man. S.E. Fl., 1341. 1933.

Herbaceous, rhizomatous, perennial. Stems erect, few to many stems, slender, from 4-8(10) dm high, pubescence appressed, silvery-sericeous. Basal leaves graminiform, silvery-sericeous, linear, acute to acuminate, 10-25 (45) cm long and 5-10 mm wide, spreading or ascending, sessile, forming a loose basal rosette, overwintering. Lower cauline leaves similar to basal leaves but reduced

upward on stem; upper cauline leaves appressed or ascending, lanceolate, sessile, below inflorescence 4-7 cm long and 2.5-6 mm wide; peduncular bracts numerous, appressed. Inflorescence open, with spreading-ascending branches to 30 in number, sometimes branched, pubescence sericeous, with 30-100(150) heads. Peduncles from 1-8(10) cm long, slender, to 0.8 mm thick, sericeous, many narrow appressed peduncular bracts 2-5 mm long which intergrade with the phyllary bracts. Heads small, cylindric, 4-6 mm wide and 5-7(8) mm high, shorter than mature pappus. Phyllaries imbricate in 5-7 series, squarose when dry, scarious; outer usually all silky-sericeous, to 2.5 mm long, linear-lanceolate; inner to 6-7 mm long, usually stipitate glandular at midnerve, fimbriate at apices. Ligulate corolla limb to 6.5 mm long and 1.6 mm wide, 8-11 in number. Disc corollas 5-6.5 mm long, 15-30 in number, slightly pilose, lobes 0.5 mm long; pappus double, outer of 12-27 setiform squamellae, 0.6-1.2 mm long; inner of 27-45 barbellate capillary bristles, 5.0-7.0 mm long. Achenes fusiform with 6-8 appressed ribs, slightly sericeous. N=9.

Flowering time: Mostly from early August to October, but in the southern states (Florida, Georgia, Alabama) sometimes in late December or early spring.

Type: Curtiss No. 5319, dry pine barrens near

Jacksonville, Florida, October 13, 1894. (NY!) (Figure 16).

Variation and ecology: H. microcephala var. microcephala is certainly abundant in the Coastal Plain where H. graminifolia is also present. It had been included under H. graminifolia by Dress (1953) but is considered as distinct in this study (see discussion under taxonomic treatment).

It could be confused with H. adenolepis, H. graminifolia, and H. microcephala var. aequilifolia. The former has already been discussed. The differences from H. graminifolia will be discussed under that entity.

The main differences between var. microcephala and var. aequilifolia are that in var. aequilifolia the cauline leaf width/length ration is .20 or more, the leaves are little reduced upward, rhizomes are absent, and the caudex is woody at the base. The two apparently grow in similar habitats; however, this study indicates that var. aequilifolia grows in very dry soil areas. The morphological differences persist into the greenhouse culture. The chromosome number is N=9, and no meiotic irregularities were noted.

H. microcephala var. microcephala has a range similar to that of H. graminifolia but is limited strictly to the Coastal Plain. No ecological differences were noted in the field trips. In Table VIII, page 56, the habitats noted are similar to H. graminifolia except for a higher frequency

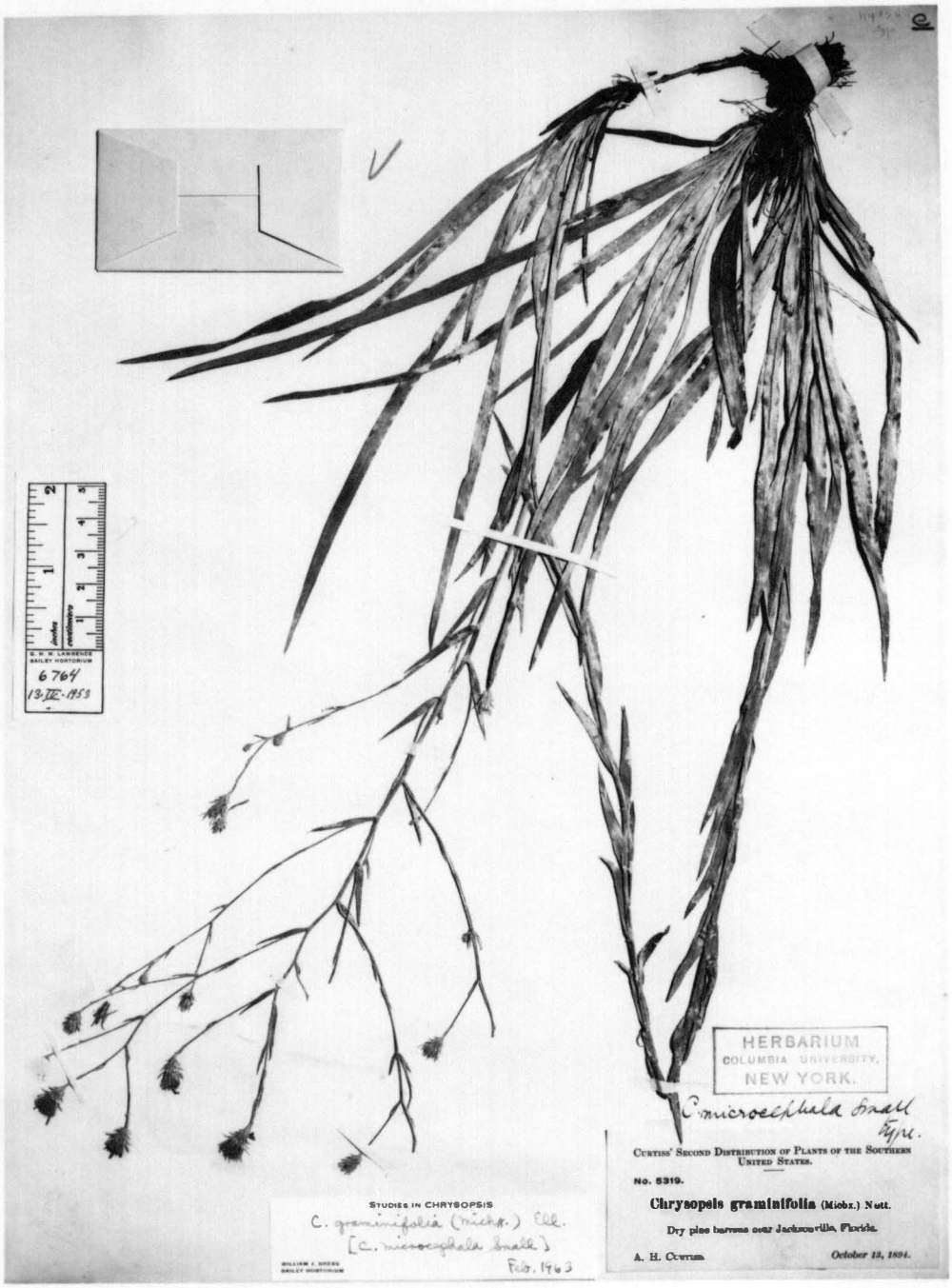

Figure 16. Type specimen of Heterotheca microcephala var. microcephala (Small) Shinners.

in the pine habitat (34 percent) compared to H. graminifolia (20 percent). Heterotheca microcephala is present in Arkansas and in southeastern Oklahoma (where H. graminifolia is absent).

Distribution: Florida northward to southeastern North Carolina, westward to Texas, southeastern Oklahoma, and Arkansas, mostly Coastal Plain (Figure 17a).

Representative specimens: A total of 702 herbarium specimens were examined along with several population study collections. The following are representative specimens: ALABAMA: Baldwin Co., McDaniel #3907 (VDB, FSU); Barbour Co., Justice and Isely #52 (US); Covington Co., Harper #4034 (NY); Escambia Co., Blanton #7065 (MO); Geneva Co., Kral #33773 (VDB); Mobile Co., Kral #29686 (VDB, NCU, SMU); Russell Co., Kral #33297 (VDB); Sumter Co., Jones #1751 (NCU); Washington Co., s. coll. s.n. (MO).

ARKANSAS: Ashley Co., Demaree #21599 (MO, SMU); Bradley Co., Demaree #18312 (MO, F); Clark Co., Demaree #54826 (SMU); Cleburne Co., Ford #120 (CU); Dallas Co., Demaree #37644 (KANU); Drew Co., Demaree #21722 (MO, GH, SMU); Garland Co., Demaree #15848 (SMU); Hempstead Co., Palmer #6847 (MO, US, F); Hot Springs Co., Palmer #26547 (MO); Howard Co., Kellogg s.n. (MO); Jefferson Co., Demaree #24100 (MO); Lafayette Co., Demaree #41909 (KANU, SMU); Lonoke Co., Demaree #17997 (F, SMU); Miller Co., Eggert s.n.

Figure 17. Distribution of Heterotheca microcephala (both varieties).

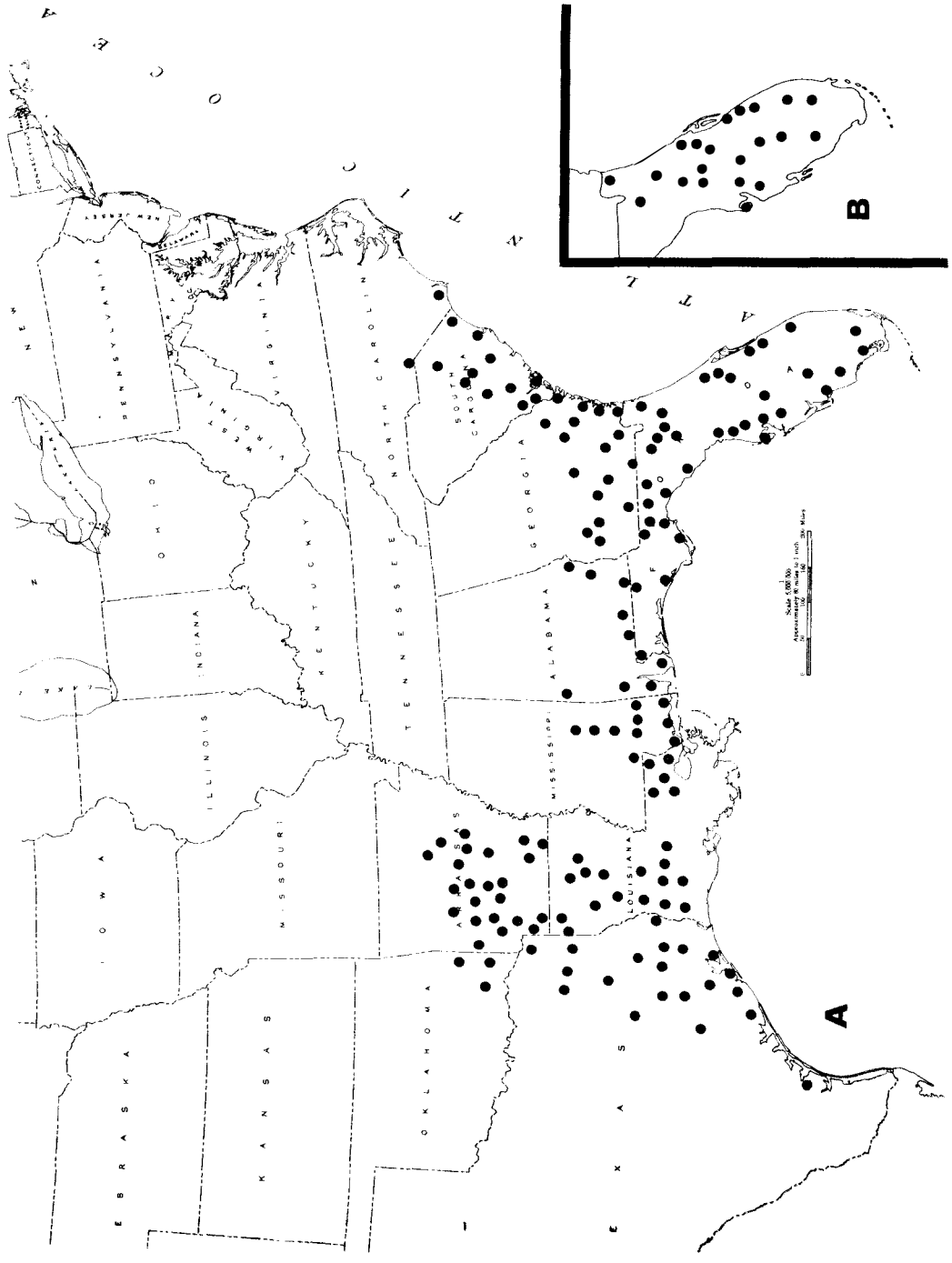
B
A
NEBRASKA
KANSAS
OKLAHOMA
TEXAS
IOWA
MISSOURI
ILLINOIS
INDIANA
OHIO
KENTUCKY
TENNESSEE
MISSISSIPPI
ALABAMA
GEORGIA
SOUTH CAROLINA
NORTH CAROLINA
VIRGINIA
PENNSYLVANIA
ARKANSAS
LOUISIANA

Figure 17

(MO, US, F); Montgomery Co., Demaree #54603 (SMU); Perry Co., Demaree #46456 (VDB); Pike Co., Demaree #9761 (GH, FSU); Polk Co., McWilliam #635 (GH); Prairie Co., Palmer #24350 (MO); Pulaski Co., Demaree #8148 (US, GH); Saline Co., Moore #420310 (TEX); White Co., Demaree #10918 (MO, GH); Yell Co., Demaree #43209 (SMU).

FLORIDA: Alachua Co., Ford #2028 (TENN); Bay Co., Billington, s.n. (US, MICH); Bradford Co., Hitchcock #893 (F); Brevard Co., Perdue #1800 (GA); Broward Co., Reis #184 (MICH); Calhoun Co., Godfrey #57910 (FSU); Charlotte Co., Jennings and Jennings #280 (USF); Citrus Co., Adams #391 (FSU); Clay Co., Murrill, s.n. (MO); Collier Co., Lakela #27710 (USF, FSU); Columbia Co., Nash #2492 (MICH, US, NY, MO, GH, P); Dade Co., Small and Nash #179 (NY); Dixie Co., Godfrey #56167 (FSU); Duval Co., Curtiss #4452 (MO, US, NY); Escambia Co., Kral and Godfrey #6031 (NY, USF); Franklin Co., McAtee #1815C (US); Glades Co., McCart #11196 (USF); Gadsden Co., Berg s.n. (NY); Hernando Co., Cooley, Ray, and Eaton #7025 (USF); Highlands Co., St. John #3422 (US); Hillsborough Co., Blanton #6808 (NY, DUKE, MICH); Holmes Co., McDaniel #5191 (FSU); Indian River Co., Kral #5305 (LAF); Jefferson Co., Godfrey #53888 (GH, NY, USF); Lake Co., Manning s.n. (NCU); Lee Co., Standley #57588 (F); Leon Co., Redfearn #1079 (FSU); Levy Co., Kral #4628 (FSU, SMU); Madison Co., Kral #3780 (GH, NY); Manatee Co.,

Tracey #6933 (MO, US); Martin Co., Moldenke #21480 (SMU); Monroe Co., Miller and Killip #31462 (US); Okaloosa Co., Godfrey #59032 (FSU); Orange Co., Nash #2313 (US); Osceola Co., Singeltary #178-a (DUKE); Palm Beach Co., Hitchcock #890 (F); Pasco Co., Barnhart #3785 (NY); Pinellas Co., Proctor #2548 (PH); Polk Co., Berry #277 (TENN); Taylor Co., Godfrey and Morrill #52551 (DUKE); Union Co., Godfrey and Morrill #52604 (FSU); Taylor Co., Godfrey and Morrill #52551 (DUKE); Volusia Co., Hood s.n. (MO); Wakulla Co., Lozoe #5092 (FSU).

GEORGIA: Berrien Co., Lemon #98446 (FSU); Bullock Co., Plummer and Pullen #904 (GA); Calhoun Co., Thorne #6873 (GA, CU, GH); Camden Co., Godfrey #50907 (NY, GH, FSU, DUKE, GA); Charlton Co., Harper #668 (PH, NY); Chatham Co., Duggar s.n. (MO); Doutherty Co., Duncan #3087 (TENN, GH, GA); Echols Co., Clewell #2632 (FSU); Glynn Co., Thorne and Muenscher #8861 (CU); Long Co., Bozeman and Radford #1903 (GA, NCU); McIntosh Co., Duncan #20655 (DUKE, NCU, GH, LSU, TEX, US, SMU); Tattnall Co., Boole #1009 (NCU, SMU); Thomas Co., Godfrey #70103 (FSU); Telfair Co., Trudell s.n. (PH); Terrell Co., Duncan #1767 (GA); Tift Co., Small s.n. (GA); Ware Co., Clewell #2543 (FSU).

LOUISIANA: Allen Parish, Shinners #22202 (SMU); Beauregard Parish, Brown, Wyland, and Rogers #8701 (LSU, GH); Bossier Parish, Trelean s.n. (MO); Caddo Parish,

Thieret #21125 (NCU, LAF); Calcasieu Parish, Shinners #25074 (DUKE); Evangeline Parish, Thieret #10264 (LAF), Shinners #24973 (SMU); Jackson Parish, Moore #7183 (VDB); Jefferson Davis Parish, Thieret #10214 (FSU, VDB, LAF, DUKE, SMU); Lincoln Parish, Moore #5381 (LSU, GH); Livingston Parish, Brown #6694 (LSU, GH, SMU); Natchitoches Parish, McWilliams #106 (FSU); Quachita Parish, Shinners #26676 (SMU); Rapides Parish, Duncan #56119 (MO); Red River Parish, Thieret #20495 (SMU, LAF); Sabine Parish, Shinners #20557 (SMU); St. Helena Parish, Allen #1272 (LSU); St. Landry Parish, Featherman s.n. (LSU); St. Tammany Parish, Ewan #17459 (MO); Tangipahoa Parish, Correll and Correll #9268 (DUKE, NY, F, GH, LSU); Vernon Parish, Brown and Lenz #8303 (LSU); Washington Parish, Ewan #19445 (USF, LAF); Winn Parish, Ewan #19872F (NCU).

MISSISSIPPI: Forrest Co., Jones #2317 (NCU); Greene Co., McLain #46937 (SMU); Jackson Co., Ray #2765 (USF); Jasper Co., McDaniel #2765 (NY, GA); Jones Co., Jones and Jones #14237 (GA); Hancock Co., Jones and Jones #14102 (SMU); Harrison Co., Langlois s.n. (NY); Marion Co., Jones #9200 (NCU); Newton Co., Ray #8373a (USF); Perry Co., Demaree #36249 (SMU, GH).

NORTH CAROLINA: Brunswick Co., Godfrey #50498 (FSU, DUKE); Richmond Co., Wooten #509 (FSU).

OKLAHOMA: Leflore Co., Stevens #2623 (GH, NY);

McCurtain Co., Waterfall #17363 (KANU, NCU); Pushmataha Co., Waterfall #8529 (TEX, NY).

SOUTH CAROLINA: Beaufort Co., Bell #4712 (SMU); Berkeley Co., Bozeman #11357 (LSU, FSU, GA, TEX, NY, NCU, SMU); Charleston Co., Godfrey #50918 (NY, SMU, FSU, DUKE); Clarendon Co., Radford #30988 (NCU); Colleton Co., Bell #4545 (NCU); Darlington Co., Eggleston #4936 (NY, GH); Georgetown Co., Godfrey and Boyce #50438 (FSU, TENN, NY, GH, SMU); Hampton Co., Bell #18245 (NCU); Horry Co., Grace s.n. (GH); Jasper Co., Dress and Moran #2533 (FSU); Orangeburg Co., Eggleston #4955 (NY); Sumpter Co., Radford #29524 (NCU).

TEXAS: Angelina Co., Cory #49753 (NY, MICH, US, GH); Austin Co., Tharp #4282 (TEX); Bowie Co., Shinners #30677 (TEX); Brazos Co., Hess s.n. (CU); Brazoria Co., Hanson s.n. (MO, NY); Chambers Co., Barrow #13 (TEX); Cherokee Co., Schael s.n. (TEX); Galveston Co., Henderson #62-1221 (FSU); Hardin Co., Turner #4611 (TEX); Harris Co., Lindheimer #89 (MO); Harrison Co., Bush #1033 (MO); Matagorda Co., Walter s.n. (TEX); Montgomery Co., Shinners #16568 (SMU); Polk Co., Palmer #6793 (MO, F); Newton Co., Cory #49773 (NY, MICH, GH, US, SMU); Nueces Co., Jones #4383 (TEX); Tyler Co., Cory #49855 (MICH, SMU); Upshur Co., Palmer #31760 (MO, TEX); Walker Co., Cory #50647 (NY, MICH); Wood Co., Reverchon #2041 (MO, NY).

4. Heterotheca microcephala var. aequilifolia var. nov.*

Similar to var. microcephala except for the following differences: Basal woody caudex present. No evident rhizomes present. Leaves crowded, numerous, spreading, cauline leaves only slightly reduced upward (sometimes wider); lower leaves 6-10 mm wide and 3.5-7 cm long; upper 6-10 mm wide and 3.5-6 cm long. Basal leaves often missing during flowering period. Involucral diameter 5.5-7 mm and 6.5-8 mm high. Phyllaries mostly glandless at apex. Inflorescence branches short, heads few to fifty. N=9.

Flowering time: Mostly from August to October.

Holotype: Wofford and Bowers #71-558. Sandy roadside on Highway 19 about 200 yards south of Junction with old 441 (Tavares), Lake County, Florida. 20 September 1971 (TENN). (Figure 18).

Variation and ecology: H. microcephala var. aequilifolia is limited to central Florida. It has been confused with H. graminifolia var. latifolia which is discussed under H. graminifolia.

This is a distinct variety which can be easily recognized in the field; characterized by stocky, overlapping cauline leaves, usually no basal leaves, and

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*Latin description is omitted to avoid possible valid publication of new names in this type of publication.

Figure 18. Type specimen of Heterotheca microcephala var. aequilifolia var. nov.

several stems from the woody caudex. The transplants in the greenhouse continued to have the characters listed above. The chromosome number is N=9. No meiotic irregularities were seen.

H. microcephala var. aequilifolia was collected rather infrequently (3 field collections and 47 herbarium specimens) (Figure 18, page 125). The data in Table VIII, page 56, is limited because of the number of specimens but indicates generally it has a similar habitat requirement to that of var. microcephala. Its range, however, does coincide with similar endemics of Florida which are mentioned by James (1961) in the lake district of central Florida which is mainly longleaf-slash pine forest. The soil is almost entirely composed of coarse to fine sandy-loamy soils (Psammaquents). This study indicates the populations are mainly in very dry sandy areas.

Distribution: Apparently only found in peninsular Florida (Figure 17, page 118).

Representative specimens: A total of 47 herbarium specimens were studied along with three mass population samples. The following are all those specimens studied: FLORIDA: Brevard Co., Leeds #416 (PH), Fredholm #5553 (GH); Broward Co., Will and Smith s.n. (GA); Collier Co., Steyermark #63285 (F), Blanchard s.n. (DUKE); Glades Co., McCart #11196 (SMU); Highlands Co., Brass s.n. (US), Ray,

Lakela, and Patman #10404 (USF), Ray, Lakela, and Patman #10371 (USF), Webster #4213 (TEX), Ray, Lakela, and Patman #10371 (GH); Indian River Co., Palmer s.n. (MO), Kral #5305 (FSU, LSU, VDB), D'Arcy #2969 (DUKE); Lake Co., Bowers and Wofford #71-557 and #71-558 (TENN), Ray, Jr. #10521 (USF), Hunnewell #8737 (GH), Turner #4672 (SMU, TEX), Hitchcock s.n. (MO, F); Lucie Co., Kral #22862 (VDB, SMU); Manatee Co., Bowers and Wofford #71-559 (TENN), Tracy s.n. (GH), Tracy s.n. (US); Marion Co., Arnold s.n. (KAN); Orange Co., Nash s.n. (F, MO, GH), Arnold s.n. (GA); Palm Beach Co., Randolph #99 (GH, NY); Pinellas Co., Deam #2749 (MO), Deam #2774 (MO); Polk Co., McFarlin #3324 (MICH), McFarlin #2982 (MICH), Schallert #19882 (SMU), Godfrey #50890 (FSU); Putnam Co., Godfrey #69220 (FSU); St. Lucie Co., Lakela #25218 (USF); Seminole Co., Schallert #19882 (KAN), Ray, Jr. #10886 (USF); Volusia Co., Hood s.n. (GH), Godfrey #50881 (FSU), Butts s.n. (GH).

5. Heterotheca graminifolia (Michx.) Shinners, Field and Lab. 19: 71. 1951.

Inula graminifolia Michx., Fl. Bor. Am. 2: 122. 1803.

Erigeron nervosum Willd., Sp. Pl., 4th ed., 1953. 1803. (Type: "Habitat in America boreali" B-photo seen)

Inula argentea Pers. Syn. Fl. 2: 452. 1807.

(Type: "Habitat in Pennsylvania," Type P (not seen), L! - Isotype.

Chrysopsis argentea (Pers.) Ell., Sk. Bot. S.C. and Ga. 2: 334. 1824.

Chrysopsis graminifolia (Michx.) Ell., Sk. Bot. S.C. and Ga. 2: 334. 1824.

Inula graminifolia Michx. Beta tenuifolia Torr., Ann. Lyc. N.Y. 2: 212. 1828. (Type: Dr. James s.n., Long's Expedition to the Rocky Mts., NY!).

Diplopappus graminifolius (Michx.) Less., Linn. 5: 144. 1830.

Diplopappus sericeus Hook., Comp. Bot. Mag. 1: 97. 1836. (Nomen nudem).

Pityopsis graminifolia (Michx.) Nutt., Trans. Am. Philos. Soc., 3.2, 7: 317. 1841.

Pityopsis argentea (Pers.) Nutt., Trans. Am. Philos. Soc., 3.2, 7: 318. 1841.

Heyfeldera sericea Bip. Schulz. Fl. 36: 35. 1853. (Type: Mexico, Vera Cruz prope Mirados in Savannis, alt. 3000 ped. Linden 1144 and 1147. Not seen.)

Diplogon graminifolium (Michx.) Kuntze, Rev. Gen. 2: 334. 1891.

Chrysopsis graminifolia var. latifolia Fern., Bot. Gaz. 24: 434. 1897. (Type: "Spruce pine land"

Jensen, Florida, Curtiss no. 5819, GH!).

C. tracyi Small, Fl. S.E. U.S. 1182. 1903. (Type: Palma Sola, Fla. S.M. Tracy, no. 7713, NY!).

P. graminifolia var. latifolia (Fern.) Small, Ibid.

Chrysopsis correllii Fern., Rhod. 44: 470. 1942. (Type: Sandy region at White Lake, Bladen County, July 15, 1935, Correll, no. 2577, GH!).

C. nervosa (Willd.) Fern., Ibid.

C. nervosa var. virgata Fern., Ibid, 474. (Type: Dry open sandy soil northwest of Magnolia Nansemond County, October 17, 1941, Fernald and Long, no. 14036, GH!).

C. nervosa var. stenolepis Fern., Ibid. (Type: Open woodland, Olympia, Pamlico County, July 12, 1922, L.F. and F.R. Randolph, no. 910, GH!).

Heterotheca nervosa (Willd.) Shinners, Field and Lab. 19: 68. 1951.

H. correllii (Fern.) Ahles, J. Elisha Mit. Sci. Soc. 80: 172-173. 1964.

H. graminifolia var. tracyi (Small) Long, Rhodora 72: 43. 1970.

Plant rhizomatous, perennial. Stems erect, solitary or up to three stems present 3-8 dm high, appressed

silvery-sericeous. Basal leaves graminiform, silvery-sericeous, 2-11 mm wide and 8-25(40) cm long, very variable in width and length, forming basal rosette, overwintering. Lower cauline leaves similar to basal except reduced upward on stem; upper cauline leaves more or less appressed to spreading, linear-lanceolate, 2-6 mm wide and 3-9 cm long; peduncular bracts appressed, subulate. Inflorescence varies from a few heads borne virgately to numerous open ascending-spreading branches with over 100 heads, silvery-sericeous. Peduncles from 1-10 cm long, slender, to 1.0 mm thick, sericeous, few to many narrow appressed peduncular bracts sometimes intergrading with phyllary bracts. Heads large, 6.5-10 mm wide and 8-13 mm high, as long as mature pappus. Phyllaries in 4-6 series, imbricate, erect, scarious margin, herbaceous center, outer subulate to lanceolate, inner linear-lanceolate 6-8 mm long, acuminate, silky-hairy, occasionally glandular at apex. Disc corollas 6.5-9 mm long, slightly pilose, lobes 0.6-0.8 mm long, 30-50 in number. Ligulate corolla limb to 7-12 mm long and 3 mm wide. Pappus double; outer of 12-25 setiform squamellae, 0.6-1.4 mm long; inner of 30-55 barbellate capillary bristles to 7(9) mm long. Achenes 2.5-4.4 mm long, fusiform to linear, obscurely ribbed (8-10), silky pubescent. N=18.

Flowering time: Generally flowers from August to

October, earlier or later in southern part of range, also may flower after injury due to burning or cutting.

Type: Michaux s.n. "Caroline, fleurit on Septembre." The type of Inula graminifolia Michx. is in the L'Herbier de Paris (P). A photograph of the type was sent to the Gray Herbarium and has been seen. Also an isotype from Paris has been examined (Figure 19). There has been confusion in the past as to the correct use of the name graminifolia. Earlier authors apparently interpreted it correctly until Fernald (1942) decided it should have been applied to the glandular peduncled taxa (H. adenolepis or H. aspera). Others have assumed it meant the smaller headed taxa (Dress, 1953) which included H. microcephala. However, from the photograph of the type with an included metric scale, the heads are too large for H. microcephala and the peduncle too pubescent to be H. adenolepis or H. aspera. Shinners and Harms (1969) both were apparently written by Dr. Marshall Johnston that the type material of Inula graminifolia was not glandular on the peduncles; therefore, it should not be applied to the H. aspera taxa. The isotype is mixed with a small stem of H. microcephala present in the middle and the others H. graminifolia (Figure 19).

Variation and ecology: Heterotheca graminifolia is probably the most abundant of all the species in section

Figure 19. Isotype of Heterotheca graminifolia (Michx.) Shinners.

Pityopsis. There has been much confusion in the past on the limits of H. graminifolia and has formerly been circumscribed to include H. graminifolia, H. adenolepis, H. aspera, H. microcephala, and H. oligantha. Dress (1953) included the first four above under H. graminifolia with four varieties. Small (1933) used four of the species, omitting only H. adenolepis (included with H. aspera).

H. graminifolia var. latifolia was described by Fernald (1897) for a stocky plant with a few large cauline leaves, no basal rosette leaves, based on a specimen collected by Curtiss #5819 (GH). This form was seen in this study and appears to be a monstrosity or an offshoot from a plant that has the stem broken (Figure 20). Similar plants were seen in a burned-over area in Florida. It has large heads similar to H. graminifolia and so is considered to be merely a growth form of it. However, in the past collectors have identified the smaller headed, large equal-leaved H. microcephala var. aequilifolia as H. graminifolia var. latifolia. It was, therefore, necessary after looking at the type of variety latifolia to give a new name to the aequilifolia plant. The differences are listed under the two varieties of H. microcephala.

H. (Chrysopsis) tracyii was described by Small

Figure 20. Type specimen of Heterotheca graminifolia var. latifolia Fern.

(1933) and C. nervosa var. virgata by Fernald (1942). The former is merely a form with a few large heads and with narrow leaves which is often found in Florida. The latter is a form with heads on a stem much like Liatris. Both are growth forms apparently; the former environmental (growing in dry, sterile conditions especially deep sandy soil), and the latter by injury to the plant. Both forms have been found in late offshoots or in adverse environments in populations of Tennessee H. graminifolia. Chrysopsis nervosa var. stenolepis and C. correllii described by Fernald (1942) also appear to be merely growth forms which can appear in many populations. The latter is based upon whether the first flowering heads being overtopped by those later and the former on whether the phyllaries are strongly herbaceous or slightly so. However, by using the characters listed and, if possible, checking pollen size (Figure 3, page 24), a correct taxonomic decision may be reached in most cases.

The chromosome number in H. graminifolia is N=18. It is one of the more difficult species to count due to clumping of chromosomes, but normal pairing does occur.

The two main entities which could be confused with H. graminifolia are H. adenolepis and H. microcephala. The former has been discussed under H. adenolepis.

H. graminifolia and H. microcephala differences

are listed in Table XIII. The main geographic areas where the greatest confusion occurs is in Florida, Arkansas, and possibly Texas. In these areas some of the H. microcephala entities are at the extremes in size and nearly reach the proportions of H. graminifolia.

H. graminifolia is wide-spread in the Coastal Plain from Florida north to Delaware and west to Texas (Figure 21) and is also present in the Cumberland Plateau in Tennessee and Kentucky north to Ohio. It also occurs in pinelands of the Bahamas, Mexico, and British Honduras. In Table VIII, page 56, it is seen that this is one of the more adaptive species in its habitat requirements. While sand is still high (40 percent) and pine and pine-oak (34 percent), it also occurs occasionally on shale (2 percent), clay (1 percent), and rocks (2 percent). The 16 percent occurrence in open (fields, savannahs) is also high. While this species covers many soil types, in general they are siliceous, dry part of the year and low in bases. Little can be said specifically of its habitats except that it mainly follows the area of Oak-Hickory-Pine and Southern Mixed Forest on the Coastal Plain.

It also occurs on the fall line of the Piedmont and north to Ohio on the Interior (Allegheny and Cumberland) Plateaus (Braun, 1939) in sandy soils. This would be a region closely following the short-leaf pine in this

Figure 21. Distribution of Heterotheca graminifolia and H. oligantha.

A. H. graminifolia (United States).

B. H. oligantha.

C. H. graminifolia (Latin America).

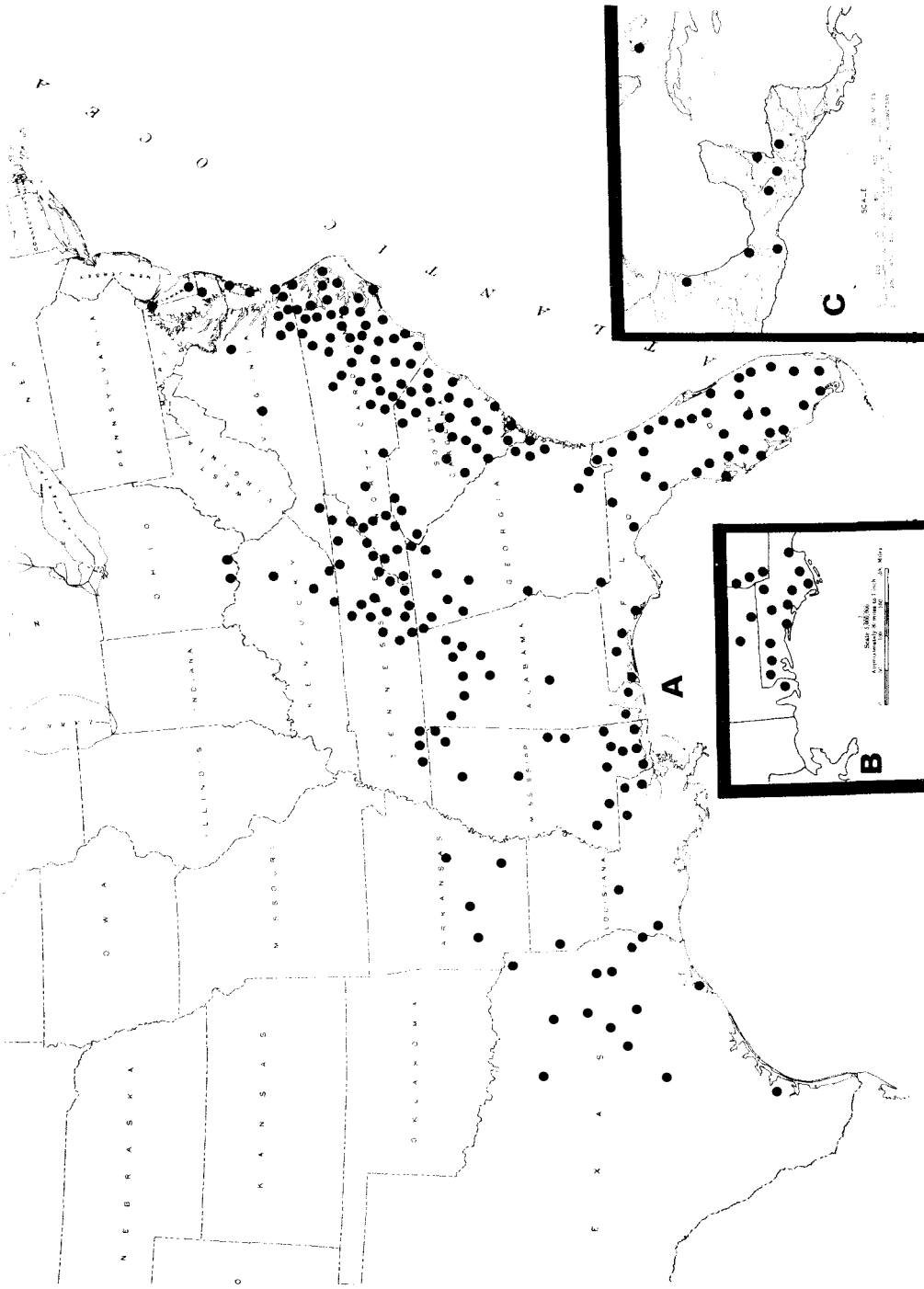

A
B
C
NEBRASKA
KANSAS
OKLAHOMA
TEXAS
ARKANSAS
LOUISIANA
MISSISSIPPI
ALABAMA
GEORGIA
FLORIDA
TENNESSEE
KENTUCKY
ILLINOIS
INDIANA
OHIO
IOWA
PENNSYLVANIA

Figure 21

area. It can occasionally be found also in shale-soil areas in the Valley and Ridge and Blue Ridge Provinces in Tennessee (Shanks, 1958), Georgia, and Alabama.

Distribution: Probably the most abundant species from Florida northward to Delaware mostly on the Coastal Plain but also in Ohio, the Cumberland Plateau of Kentucky and Tennessee and west on the Coastal Plain to Texas; disjunctly present in southern Mexico, Guatemala, British Honduras, and the Bahamas (Figure 21a and c, page 137).

Representative specimens: More than 800 herbarium specimens were examined along with several population samples. The following are representative specimens: ALABAMA: Autauga Co., Harper #3270 (GH, MO, PH, NY); Baldwin Co., Wofford #10193 (NCU); Cullman Co., Eggert s.n. (MO); Dallas Co., Perdue #4153 (FSU, US); DeKalb Co., Henry #5036 (PH); Etowah Co., s. coll. #1955f (PH); Franklin Co., Kral #32920 (VDB); Jefferson Co., Kral #33607 (VDB); Marshall Co., #1957d (US); Mobile Co., Demaree #34523 (NY); St. Clair Co., Bostick #209-5 (NCU); Winston Co., Eggert s.n. (NY, MO).

ARKANSAS: Drew Co., Demaree #21722 (MO, SMU); Hot Springs Co., Palmer #26547 (NY, MO); Pike Co., Demaree #9761 (MO, GH, SMU, MICH); Prairie Co., Demaree #54752 (SMU).

DELAWARE: Castle Co., Canby s.n. (F); Surry Co., Commons s.n. (PH); Sussex Co., Canby s.n. (NY).

FLORIDA: Alachua Co., Murrill #155 (US); Bay Co., Godfrey #59135 (FSU); Brevard Co., Fredholm #5567 (GH); Broward Co., Lakela #28333 (USF); Charlotte Co., Adams #174 (FSU); Collier Co., Lakela #27793 (USF); Columbia Co., Quaintace #390 (F); Dade Co., Dowell #344 (GH); Duval Co., Curtiss s.n. (GH); Escambia Co., Benke #3233 (US, F); Flager Co., Ames #233 (NY, GA); Glades Co., Lovett and Oosting #182 (DUKE); Hamilton Co., Hager s.n. (NY); Hernando Co., Ray, Jr. #9570 (USF); Highlands Co., Small #9015 (NY); Hillsborough Co., Lakela #24800 (USF); Lee Co., Standley #18878 (US); Levy Co., Godfrey and Clewell #64765 (FSU); Manatee Co., Tracy #7713 (MO, CU); Martin Co., Burch #1059 (MO, TEX); Merritt's Island Co., Small, Small, and DeWinkeler #10791 (NY, DUKE, UT); Monroe Co., Killip #40064 (MICH); Nassau Co., Small and DeWinkeler #9701 (NY); Okeechobee Co., Small and Small #4362 (NY); Okaloosa Co., Godfrey #59055 (FSU); Orange Co., Tracy s.n. (CU); Osceola Co., Singeltory #178 (DUKE); Palm Beach Co., Cassen #245 (NCU); Pasco Co., Barnhart #2875 (NY); Pinellas Co., Godfrey #50841 (GH, DUKE); Polk Co., Lakela #23835 (SFU); Putnam Co., Godfrey #69170 (FSU); Sarasota Co., Rusby s.n. (NY); Seminole Co., Schallert #3672 (KANU); St. Lucie Co., McCart #10, 559 (SMU); St. Johns Co., Godfrey and Morrill

#52636 (FSU); Taylor Co., Lazor #4638 (FSU); Volusia Co., Duncan #4611 (GA); Walton Co., Kurz s.n. (FSU).

GEORGIA: Bartow Co., Greear #64503 (NCU, GA); Bryan Co., McKay s.n. (GA); Charleston Co., Duncan #5855 (GA); Charlton Co., Proctor #21 (GA); Chatham Co., Boole #1048 (NCU); Dade Co., Cronquist #5822 (GA, SMU); Dawson Co., Cronquist #4743 (PH, GH); Effingham Co., Boole #1038 (NCU, GH); Fulton Co., Henry #3890 (PH); Habersham Co., Reade #E8676 (GA); Liberty Co., Wiegand and Manning #3187 (CU); Muscogee Co., Bryan #E2151 (GA); Polk Co., Lipps and Demaree #51723 (SMU); Rabun Co., Radford s.n. (NCU); Seminole Co., Duncan #4605 (GA); Walker Co., Cronquist #4812a (NY); Ware Co., Wright and Harper #1082 (CU).

KENTUCKY: Bell Co., Freer #2030 (NCU), Kearney #405 (NY, F, GH, MO, US); McCreary Co., McFarland and Rogers #85 (NY, PH, GA, DUKE, GH, MICH, MO, SMU).

LOUISIANA: Caddo Parish, Gregg s.n. (MO); Calcasieu Parish, Brown, Nyland, and Rogers #8624 (LSU); Rapides Parish, Brown #6824 (LSU); St. Helena Parish, Thieret #24883 (LAF); St. Tammany Parish, Thieret #28337 (LAF); Washington Parish, Shinners #28803 (SMU).

MARYLAND: Wicomico Co., Moyer #2667 (NY), Wherry and Pennell #12822 (NY, F); Worcester Co., Gleason s.n. (DUKE).

MISSISSIPPI: Attala Co., McDougall #1144 (US);

Clarke Co., Schuchut s.n. (NY); Franklin Co., Brown #22068 (LSU); Greene Co., Stone #1315 (DUKE); Hancock Co., Demaree #36297 (VDB); Harrison Co., Demaree #36239 (NY, VDB, SMU); Jackson Co., Demaree #36228 (NY, FSU, VDB, SFU); Lafayette Co., Pullen #63121 (GA); Lamar Co., Jones #2601 (NCU); Lauderdale Co., Jones #10636 (NCU); Perry Co., Demaree #36249 (NY); Pike Co., Jones #9259 (NCU, GA); Prentiss Co., Iseley #4526 (SMU); Stone Co., Pullen #63127 (NCU); Tishomingo Co., Jacob #1414 (NCU).

NORTH CAROLINA: Beaufort Co., Radford #42008 (NCU); Bertie Co., Ahles #52104 (NCU); Bladen Co., Godfrey #5985 (GH); Brunswick Co., Godfrey #48447 (DUKE, KANU, GH, GA, SMU, TENN, NCU, FSU); Buncombe Co., Britton s.n. (NY); Burke Co., Bell #15052 (NCU); Cartaret Co., Godfrey #49970 (US, FSU); Cherokee Co., Radford #17605 (NCU); Chowan Co., Ahles #50914 (NCU); Columbus Co., Bell #15919 (NCU); Craven Co., Radford #40144 (NCU); Cumberland Co., Ahles #33396 (NCU); Currituck Co., Godfrey and Fox #51011 (DUKE, FSU); Dare Co., Godfrey and Fox #51047 (FSU, NY, GH, DUKE); Duplin Co., Ahles #35699 (NCU, TENN); Durham Co., Orr #370 (TEX); Edgecombe Co., Radford #40653 (NCU); Gates Co., Ahles #51581 (NCU); Greene Co., Radford #40409 (NCU); Halifax Co., Ahles #20792 (KANU, NCU); Harnett Co., Godfrey and Fox #50518 (MO); Henderson Co., Small and Huger s.n. (NY); Hertford Co., Ahles #52220 (NCU); Hoke Co., Godfrey and Fox #50547 (VDB,

FSU, DUKE, SMU); Hyde Co., Radford #42660 (NCU); Jones Co., Radford #40015 (TEX, NCU); Johnston Co., Godfrey and Fox #12049 (GH, DUKE, GA); Lenoir Co., Radford #31616 (GA, NCU); Macon Co., Godfrey #52166 (NY, SMU, DUKE); Madison Co., Ahles #50594 (NCU); Martin Co., Godfrey and Fox #50686 (US, MO, GH, NY, FSU, SMU, GA, TENN, DUKE); Mecklenburg Co., Ramsey #33187 (SMU, TENN); Moore Co., Godfrey #50714 (DUKE); Nash Co., Ahles #21196 (VDB, NCU); New Hanover Co., Bell #15963 (NCU); Northampton Co., Ahles #52422 (NCU); Onslow Co., Wood #6510 (GH); Pamlico Co., Radford #42326 (NCU); Robeson Co., Terrell #2983 (NCU); Richmond Co., Gupton #667 (NCU); Pitt Co., Correll #1395 (DUKE); Pender Co., Godfrey and Fox #48712 (NCU, KANU, GH, GA, SMU, TENN, DUKE, FSU); Sampson Co., Godfrey #4525 (GH); Scotland Co., Correll #1168 (GH); Swain Co., Raper and Jennison #3408 (TENN); Transylvania Co., Mowbray #161988 (DUKE); Tyrrell Co., Radford #42547 (NCU); Wake Co., Godfrey #48533 (DUKE); Washington Co., Radford #42434 (NCU); Wayne Co., Godfrey #6555 (US, DUKE, GH); Wilson Co., Radford #40744 (US, NCU).

OHIO: Adams Co., Bartley #1459 (US); Scioto Co., Stephenson s.n. (MO).

SOUTH CAROLINA: Aiken Co., Russell s.n. (US); Allendale Co., Bell #5120 (NCU); Bamberg Co., Ahles #37652 (NCU); Beau Co., Bell and Ahles #20931 (NCU); Beaufort Co., s. coll. #1955g (US); Berkeley Co., Ahles #35548 (NCU);

Calhoun Co., Ahles #35372 (NCU); Charleston Co., Godfrey #50915 (FSU); Chesterfield Co., Duke #1244 (NCU); Claredon Co., Radford #28059 (NCU); Colleton Co., Wiegand and Manning #3186 (GH); Darlington Co., Eggleston #4938 (MO); Dillon Co., Ahles #37062 (NCU, TENN); Dorchester Co., Ahles and Haesloop #37779 (NCU); Florence Co., Bell #10670 (NCU, USF); Georgetown Co., Godfrey #50909 (MO, SMU, NY, GH, DUKE, FSU); Greenville Co., Wherry s.n. (NCU); Horry Co., Wherry #7127 (US, GH); Jasper Co., Ahles #18089 (NCU); Lexington Co., McGregor #563 (US); Marion Co., Bell #11007 (NCU); Marlboro Co., Duke #1793 (NCU); Oconee Co., Freeman #58489 (NCU); Orangeburg Co., Eggleston #49549 (NY); Spartanburg Co., Seymour #4168 (US); Sumter Co., E.B.B. #3239 (US); Williamsburg Co., Godfrey and Tryon, Jr. #511 (GH).

TENNESSEE: Blount Co., Thomas #32998 (TENN); Bradley Co., Ruth #606 (NY); Claiborne Co., s. coll. #1955 (US); Cocke Co., Anderson #1115 (GH); Cumberland Co., Morton #1414 (TENN, SMU); Fentress Co., Cain s.n. (TENN); Grundy Co., Clark #2074a (NCU); Hamilton Co., Ward s.n. (GH, MO); Hardeman Co., Sharp and McLaughlin #16934 (TENN); Hardin Co., Rogers #40074 (TENN, KANU); Hawkins Co., Iltis #1649 (TENN); Marion Co., Russell and Ford #2251 (TENN); McNairy Co., Shanks, Clebsch, and Woods #14706 (GA, TENN); Monroe Co., Rogers #42292 (TENN, NY); Morgan Co., Svenson #4096

(GH); Polk Co., Wherry and Pennell #14014 (MO, PH); Rhea Co., Cooley, Woods, and Shanks #13968 (TENN); Sevier Co., Chandler #4529 (MO); Sullivan Co., Shanks #1134 (TENN); Unicoi Co., Price #1058 (DUKE); Van Buren Co., Ford and Russell #1986 (TENN).

TEXAS: Anderson Co., Calley and Marsh #93 (SMU, TEX); Angelina Co., Shinners #26796 (SMU); Bastrop Co., Warncock and Albers #45-151 (SMU, TEX); Bowie Co., Ward s.n. (US); Galveston Co., Turner #3695 (TEX); Jasper Co., Shinners #7639 (SMU); Leon Co., Turner #1571 (SMU); Nacogdoches Co., Shinners #24882 (SMU); Newton Co., Mahler and Weaver #5196 (SMU); Nueces Co., Jones #1291 (SMU); Robertson Co., Tharp and Barkley #13977 (TEX, F, FSU); Tarrant Co., Ruth s.n. (TEX); Tyler Co., Cory #54904 (SMU); Walker Co., Cory #50647 (GH, US, SMU); Walker Co., Correll #38079 (SMU); Van Zandt Co., Reverchon and Bell #439 (F).

VIRGINIA: Accomark Co., Harvill #15099 (NCU); Amherst Co., Steele s.n. (US); Carolina Co., Iltis #911 (DUKE); Isle of Wright Co., Harvill #17917 (NCU); Nansemond Co., Fernald and Long #11456 (GA, TENN); Norfolk Co., Kearney, Jr. #2393 (US); Northhampton Co., Fernald, Long, and Fogg #5503 (PH); Princess Anne Co., Fernald and Long #15369 (NY); Southhampton Co., Fernald and Long #9636 (PH); Sussex Co., Fernald and Long #12859 (PH); Washington Co., Sharp s.n. (MO); Wythe Co., Shriver #1859 (PH).

BRITISH HONDURAS: El Cayo District, Hunt #7 (US); Jenkins Creek, Gentle #4091 (US, MICH, F); San Agustin, Lundell #6630 (MICH); Mt. Pine Ridge, Lundell #6630 (TEX, US); El Cayo District, Molina #169 (F).

BAHAMAS: Eight Mile Rocks, Britton and Millspaugh #2397 (F, US), Brace #3672 (F, US); Britton and Millspaugh #2669 (F); Grand Bahama, Webster #10873 (US).

GUATEMALA: Jocotán, Steyermark #31650 (US, F); Sierra de los Cuchumatanes, Steyermark #51800 (US, F); Democracia, Steyermark #51089 (US); Monte Virgen, Steyermark #42894 (F); Volcan de Monos, Steyermark #42294 (F).

HONDURAS: Las Casitas, Standley #29036 (F).

MEXICO: State of Chiapas, King #3111 (TEX), Purpus #9119 (MO, F), Laughlin #1215 (MICH), Nelson #2989 (US), Nelson #2911 (US), Nelson #3491 (US), Roe, Roe, and Mori #957 (MICH); Oaxaca, King #788 (MICH), King #692 (MICH), Nelson #856 (US), Purpus #12086 (F), Williams #9835 (F); Tamaulipas, Dressler #2405 (MO, MICH); State of Vera Cruz, Purpus #1847 (MO, US, F); Zacuapam, Purpus #10853 (US).

6. Heterotheca ruthii (Small) Harms, Castanea 34: 402-409. 1969.

Chrysopsis ruthii Small, Bull. Torr. Bot. Club 24: 493. 1897.

Pityopsis ruthii (Small) Small, Man. S.E. Fl., 1341. 1933.

Plant perennial, with underground rhizomes spreading from a woody rootstock. Stems erect, numerous, 1-3 dm high, slender, densely silvery-sericeous, glabrate with age. Overwintering basal leaves linear-lanceolate, 3-4 cm long and 3-4 mm wide, sericeous pubescence. Cauline leaves numerous and overlapping, ascending-spreading, 3-5 cm long and 2-4.5 mm wide, linear to oblong lanceolate, sessile, acuminate, silvery-sericeous both surfaces, lower leaves deciduous late summer. Inflorescence of 1-8 pedunculate heads per stem terminally produced or from uppermost leaf axils. Peduncles from 0.5-3.5 cm long and 0.6-1.0 mm wide, densely stipitate-glandular (light colored) with few to-mentose hairs, 0-3 short, lanceolate, bracteoles. Heads 5-7.5 mm wide and 6-8 mm high, campanulate-turbinate. Phyllaries in 4-6 series, ascending, lanceolate, acuminate, scarious but herbaceous centrally, glandular with light colored stipitate to sessile glands, ciliate at apex and edge; outer 0.4-0.8 mm wide and 2-3.4 long, outer 0.6-0.9 mm wide and 5-7 mm long, as long as mature pappus. Ligu-late corolla limb from 6-8 mm long, 9-14(18) in number. Disc corollas 4.5-6.5 mm long, 30-45 in number, slightly pilose, lobes 0.6 mm long. Pappus double; outer of 17-32 setiform squamellae, 0.2-0.8 mm long; inner of 25-37 barbellate capillary bristles, 4.2-6 mm long. Achenes fusiform with 6-8 appressed ribs, slightly sericeous. N=9.

Flowering time: August through October.

Type: A. Ruth 7, rocks, Hiwassee Valley, East Tennessee, October, 1895. (NY!) (Figure 22).

Variation and ecology: Heterotheca ruthii apparently has limited variation judging from the field collections and herbarium specimens. It is clearly separated from the other species. It was mentioned further in Phylogeny (Chapter V, page 58), but it appears to be between the H. graminifolia group and the H. pinifolia group with the sericeous appearance of the former and the stature and general growth habit of the latter. It is a diploid with a chromosome number of N=9. No meiotic irregularities were seen except for one count which showed a possible "b" chromosome.

H. ruthii has the most limited ecological and distributional range of the species found in section Pityopsis. Only collected by two people until 1971 (Albert Ruth, in the period from 1894-1902 and W. J. Dress in 1953), it has been thought to be extinct (Harms, 1969). While there are hundreds of plants of H. ruthii in the locality where it grows, there is some question as to its ability for continued existence (Bowers, 1972). It is apparently a pioneer species in this locality. The plants are found growing in soil on flat surfaces and crevices of phyllite rocks in or within 50 feet of the Hiwassee River in Polk

Figure 22. Type specimen of Heterotheca ruthii (Small) Harms.

County, Tennessee along a 1-1/2 mile stretch of river. The rocks apparently supply no special requirement as seedlings and transplants of H. ruthii grow normally in the greenhouse in a potting media of 1/2 loam and 1/2 sand. The river has been dammed, diminishing water flow but before this, the river must have been fairly often inundated and the river rocks scoured more frequently. The damming may prevent open areas for "pioneer" H. ruthii to become established and eventually may cause its extinction if it cannot compete with the later invaders such as Aster linariifolius L., Andropogon ternarius Michx., et cetera (Bowers, 1972).

Distribution: Limited to the Hiwassee River Gorge in Polk County, Tennessee (Figure 23). At present it has been found only along the river for a distance of 1 to 1-1/2 miles centered around the site of McFarland (an old railroad siding).

Representative specimens: A total of 19 herbarium specimens were examined along with some representative population studies. The following are all the specimens examined:

TENNESSEE: Polk Co., Bowers, Sharp, Skorepa #45627 (TENN), Bowers and Odenwelder #45573 (TENN), Ruth s.n. (NY, MO, NCU), Dress #2617a (NY, FSU, CU), Ruth #608 (NY), Ruth s.n. (US), Ruth #1501 (US), Ruth #622 (US), Ruth #26 (GH), Ruth #651 (MO).

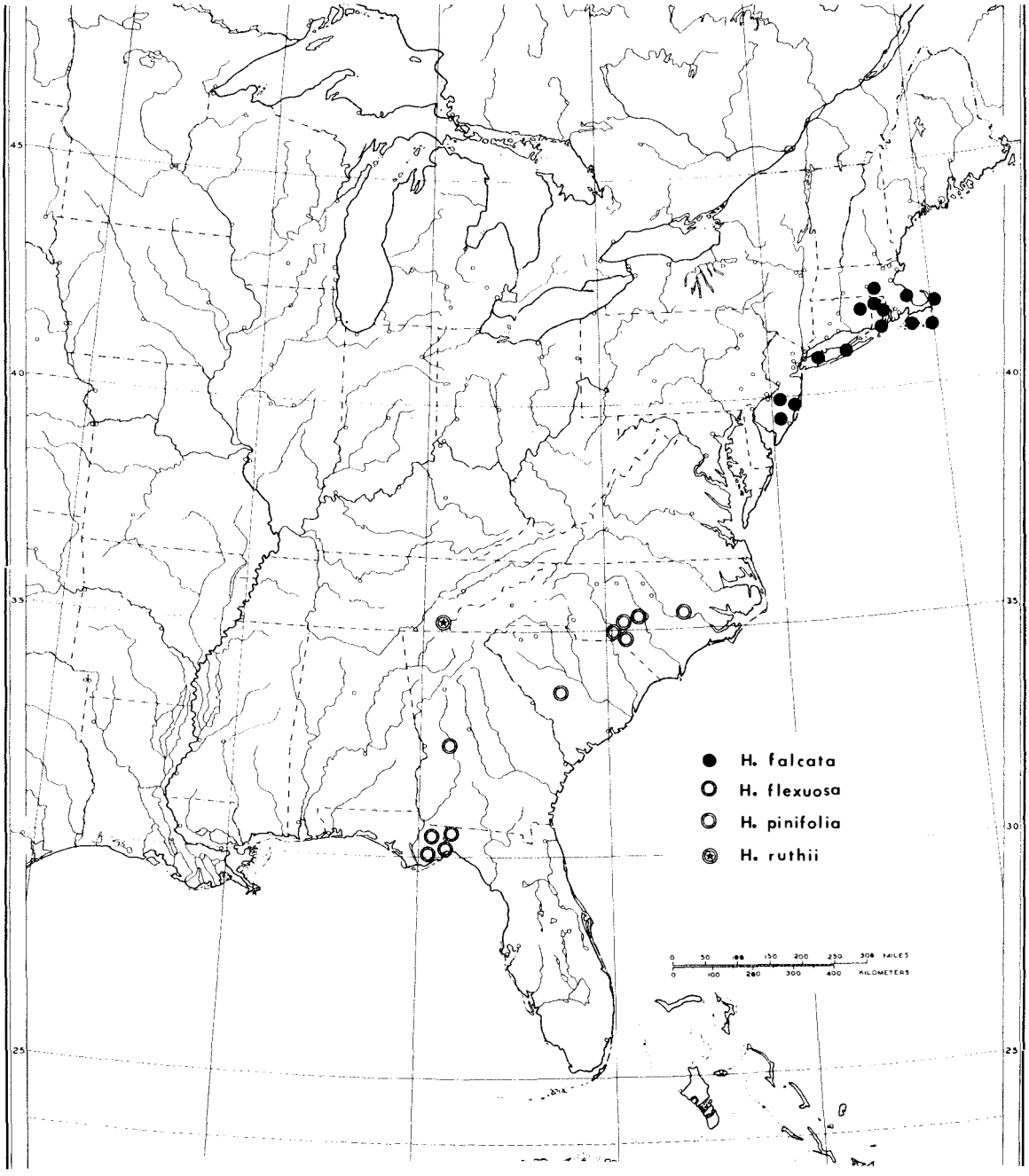


Figure 23. Distribution of Heterotheca falcata, H. flexuosa, H. pinifolia, and H. ruthii.

7. Heterotheca oligantha (Chapm.) Harms, Wrightia 4: 11. 1968.

Chrysopsis oligantha Chapm. ex Torr. and Gray, Fl. N. Am. 2: 253. 1843.

Phyopsis oligantha (Chapm.) Small, Man. S.E. Fl., 1341. 1933.

Plant perennial, rhizomatous. Stems usually solitary, erect, slender 4.5-6 dm high, silvery-sericeous lower one-third of stem, upper two-thirds glandular with dark stipitate glands. Basal leaves silvery-sericeous, graminiform, 3-14 mm wide and 8-27 cm long, forming basal rosette, overwintering. Lower cauline leaves few in number (2-4), 4-11 mm wide and 6-11(15) cm long, sericeous; upper cauline leaves reduced in size, few in number (2-4), 2-5 mm wide and 1-5 cm long, sericeous; cauline leaves remote, clasping, linear to broadly oblanceolate, acute, sometimes broader than basal leaves. Inflorescence open, ascending, of a few long (some short) peduncles from 2-14 cm long and 0.8-1.2 mm wide, stipitate glandular similar to stem, occasional tomentose hairs; bractioles few in number (1-4), minute, 2-4 mm long. Heads large, 8-11 mm wide and 9-11 mm high, campanulate. Phyllaries in 4-5 series, imbricate, erect, scarious margin, herbaceous center, glandular with stipitate dark glands; outer linear to 3.5 mm long; outer linear-lanceolate to 9 mm long. Ligulate corolla limb 9-13 mm long

and to 4 mm wide, 11-16 in number. Disc corollas 6.5-8 mm long, 26-40 in number, slightly pilose, lobes 0.6-0.8 mm long. Pappus double; outer of 15-26 setiform squamellae, 0.8-1.4 mm long; inner of 25-40 barbellate capillary bristle to 7.5 mm long. Achenes to 4.5 mm long, fusiform to linear, obscurely ribbed, sericeous. N=18.

Flowering time: The only spring flowering taxa in section Pityopsis, the main season is from March through early June, however some flower as late as October. The earliest flowering dates may be induced by burning or injury to the plant.

Lectotype: Chapman s.n., unusually robust, damp barrens (Florida), April and May (NY). This was chosen by Dress (1953) although never published. I see no reason for not accepting this specimen as lectotype as it was collected by Chapman and was available to Torrey and Gray at the time (Figure 24).

Variation and ecology: It is the only consistent spring-flowering species (this character sometimes occurs in other species as a result of disturbance or injury to the plant). Flowering starts in March, is mainly in April and May, and tapers off to a few blooming plants in the fall months. The other species generally flower from July to October. It is found in usually moist flat lands of peninsular Florida, southern Alabama, and southwestern

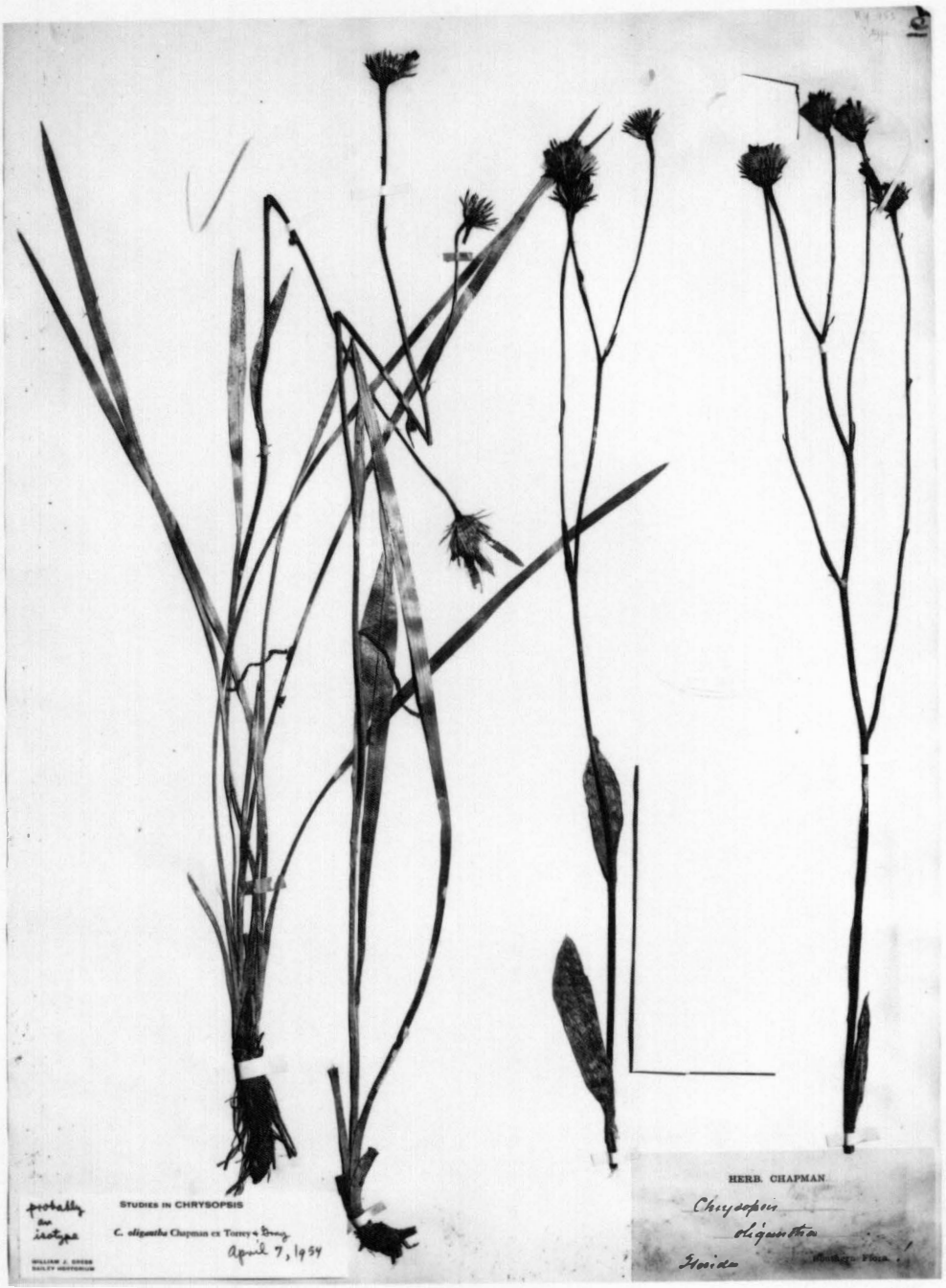


Figure 24. Lectotype of Heterotheca oligantha (Chapm.) Harms.

Georgia (Figure 21, page 137). The habitats noted on labels and through field observations are normally flat, moist pine woods or open boggy areas. This taxon grows in a region of Red-yellow Podozolic soils (Poleudults and Paleudults plus Quartzipsamments). These two characters (spring blooming and habitat requirements) probably keep this entity distinct from H. graminifolia with which it hybridizes readily in the greenhouse. The two species can be seen growing fairly close together in the field but only two or three herbarium specimens were seen which might be considered hybrids. A number of herbarium labels indicated burned areas and, in fact, over 50 percent of the plants showed signs of being burned. In field collecting, spring flowering H. graminifolia were found in burned-over areas which would permit successful hybridization taking place between the two species. It differs from H. graminifolia in having few cauline leaves (3-5), the stem being glandular almost to the base, and few large heads, usually less than 5 or 6. The glandular peduncles with a few small bracteoles make up a large proportion of the total height of the plant. A growth form of H. graminifolia is found scattered throughout the range of H. oligantha and is apparently a late offshoot or a plant grown under deep sterile sand conditions which has few heads, but it usually has very narrow leaves and a pubescent stem which would

distinguish it from H. oligantha. This has been called H. tracyii or H. graminifolia var. tracyii in Florida.

The other entity with which H. oligantha could be confused is H. adenolepis. However, H. adenolepis has small heads, shorter ligules (5 mm compared with 10 mm), many cauline leaves, short peduncles, and a stem usually pubescent and non-glandular. A few herbarium specimens have mixed collections of both species which are readily separated. One of the problems that does occur is the collection of late offshoots of H. adenolepis which superficially resemble H. oligantha. Again while the heads may be larger, they are still shorter (7 mm or less) than those of H. oligantha (8 mm or more). Also the peduncles while being glandular are smaller in diameter (4-8 mm) than those of H. oligantha (8-12 mm).

Also when tops of both H. adenolepis and H. graminifolia are burned off in the late winter or early spring, these species will bloom as early as April or May. These plants following burning are much shorter than the normal 2-3 dm height, have fewer cauline leaves and heads, and, therefore, could be confused with H. oligantha; but again anyone familiar with the three species would have no difficulty in separating them using the characters noted above.

Dress (1953) and Torrey and Gray (1843) mention specimens of H. graminifolia from Mexico which superficially

resemble H. oligantha. None were seen in this study which appear more than few-headed forms of H. graminifolia. Occasionally even H. graminifolia has glands on the peduncle, but usually these cannot be seen because of the pubescence which late in the season is often shed leaving the glands visible but restricted to the peduncle near the heads.

H. oligantha has a chromosome number of N=18 and no meiotic irregularities were seen.

Distribution: Limited to southern Alabama, the panhandle of Florida, and southwestern Georgia.

Representative specimens: More than 175 herbarium specimens were examined along with two population samples. The following are representative of the specimens examined: ALABAMA: Baldwin Co., Webster and Wilbur #3531 (NY); Covington Co., Kral #32072 (VDB), Kral #20631 (VDB); Geneva Co., Harper #101 (GH, MO, US).

FLORIDA: Bay Co., Rapp #32 (NY); Calhoun Co., Kral #4295 (LSU, GH, SMU, VDB, FSU); Escambia Co., Gaines #236 (NY); Franklin Co., Saurman s.n. #1867 (NY, PH); Gulf Co., Ahles #10265 (NCU); Jackson Co., Godfrey #63611 (FSU); Holmes Co., McDaniel #4554 (FSU); Liberty Co., Norris #656 (FSU); Okaloosa Co., Blanton #6552 (MICH, F); Wakulla Co., Kral #4162 (GA, LSU, LAF, GH, SMU, NCU, DUKE, TENN); Walton Co., Godfrey and Harrison #55400 (TENN).

GEORGIA: Early Co., Thorne #4971 (CU); Miller Co., Thorne #3429 (GA); Seminole Co., Hansen #2030 (GA).

8. Heterotheca falcata (Pursh) Harms, Castanea 34: 408. 1969.

Inula falcata Pursh, Fl. Am. Sept. 532. 1814.

I. mariana, B. falcata (Pursh) Nutt., Gen. N. Am. Pl. 2: 151. 1818.

Chrysopsis falcata (Pursh) Ell., Sk. Bot. S.C. and Ga. 2: 336. 1824.

Pityopsis falcata (Pursh) Nutt., Trans. Am. Philos. Soc. 3.2, 7: 318. 1841.

Plant perennial, rhizomatous with short rhizomes. Stems erect (10)18-27(42) cm high, one to many stems, sometimes branched above, striate, sometimes flexuous, pubescent with long sericeous hairs which become detached but do not always fall from the stem, stem somewhat purplish. Basal leaves usually absent at anthesis, overwintering, smaller than basal leaves. Cauline leaves numerous, falcate, often conduplicate, linear, acuminate, sessile, ascending to spreading, lower leaves lightly white-sericeous both sides (glabrate with age), upper leaves with pubescence along leaf margin, otherwise almost glabrate, lower leaves 3-5 mm wide and 6-9 cm long, deciduous with age, upper leaves little difference in size. Inflorescence an open cymose-panicle, branched above, with 5-25 heads per

stem; slender peduncles .4-.8 thick, 1-4 cm long, white villous pubescence also light colored, minute, stipitate glands, short-lanceolate bracteoles 0-4 in number. Heads small, campanulate-turbinate or turbinate, 5-8 mm high and 6-8 mm wide. Phyllaries imbricate in 4-6 series; outer broad lanceolate 2.0-3.8 mm long; inner linear-lanceolate to 7 mm long. Disc corolla 4.5-6 mm long, 35-50(65) in number, lobes 0.5 mm long, tube slightly pilose. Ligulate corolla 11-15 in number, ligules 5.5-8 mm long. Pappus double; outer of 18-26 setiform squamellae to 1.0 mm long; inner of barbellate capillary bristles to 5.5 mm long. Achenes fusiform, linear ribbed, sericeous. N=9.

Flowering time: July through September.

Type: Pursh apparently described this species from a specimen of Banks. "In sandy pine woods, New Jersey." It has not been found at Philadelphia or at Kew (possible repositories of Pursh specimens according to Hitchcock, 1934). No specimen was found at Paris, Geneva, and the British Museum. Rather than designate a new type, further searching should be done in European herbaria. His description (Pursh, 1814);

> Inula lanata-villosa; folias sessilibus linearibus acutissimus subfalcate-patentibus nervosis utrinque pilosis, pedunculis paucis axillaribus corymbosis calycibusque villensis. . . .

Since only H. mariana and H. falcata occur in that

area, the description matches that of H. falcata. Pursh had just described Inula mariana before this species so he scarcely could have confused the two. (Representative specimen, Figure 25).

Variation and ecology: Heterotheca falcata is characterized by its (1) falcate, linear crowded leaves, (2) pubescent (villous) stems becoming glabrate with age, (3) numerous medium-sized heads, and (4) a number of stems arising from short rhizomes. With the exception of slightly broader leaves in the New Jersey pine barrens, this taxa represents a rather uniform species ranging from New Jersey to Long Island and Martha's Vineyard (Figure 23, page 151). It is not usually confused with any of the other species in section Pityopsis. Heterotheca mariana is the only other Heterotheca at present in its range, but H. mariana has much broader leaves and the broader flattened achenes.

The three H. falcata sample areas checked cytologically were diploid with a chromosome number of N=9 (Table III, page 24). No meiotic irregularities were seen in this entity.

In the pine barrens it occupies open areas in sand soil in pine woods (Pinus rigida and P. echinata). The three sites of collections by the author (Bowers, 72-205, 210, 215) were in almost pure sand with little gravel. No plants were seen in nearby gravelly areas. It also

Figure 25. Representative specimen of Heterotheca falcata (Pursh) Harms.

occurs in areas where the plants are thought of as being adventive. It is reported along the Canadian Railway tracks west of Toronto, Ontario (Cody, 1952). Herbarium labels indicate it is found in similar sites in Rhode Island and New York. One herbarium specimen (Gunnison, no. 2593) indicated it was collected in 1955 along the beach at St. Petersburg, Florida. It indicated hundreds of plants were seen. However, in the spring of 1972, no plants were seen by the author along this beach.

H. falcata (Figure 23, page 151) is found in the northeastern Coastal Plain region. In the New Jersey pine barrens they occur on coarse acid sand soils (Lakewood and Sassafras) as described in Tedrow (1963) in pitch pine regions (Harshberger, 1916). These would be classified under Podozol soils (Lakewood) or Red-yellow Podozolic (Sassafras) (Tedrow, 1963). On Long Island and Cape Cod, the plants grow on sands behind the beach sands (Dress, 1953). In general these soils are well drained, low in nitrogen, and droughty (Harshberger, 1916). In Table VIII, page 56, sand (70 percent) and pine (27 percent) are the most frequently mentioned habitat observations.

Distribution: Pine barrens, fields, and beaches of the Atlantic Coast, from the pine barrens of New Jersey north to Long Island, New York, and Cape Cod, Massachusetts.

Representative specimens: A total of 378 herbarium

specimens of this species were studied. The following are representative specimens: CONNECTICUT: Fairfield Co., Winton s.n. (GH); New Haven Co., Horger #1257 (PH).

MASSACHUSETTS: Barnstable Co., Fernald and Long #19177 (PH); Dukes Co., Fernald #31 (F, MO, GH, MICH, GA, PH, SMU); Nantucket Co., Sargeant s.n. (SMU); Plymouth Co., Blake #10763 (F); Worcester Co., Seymour and Eaton #20500 (SMU).

NEW JERSEY: Atlantic Co., Killip #13283 (US); Burlington Co., Long #57327 (PH); Ocean Co., Grove #818 (PH).

NEW YORK: Nassau Co., House #9638 (CU); Suffolk Co., Muenscher and Curtis, Jr. #6557 (PH, GH, CU).

RHODE ISLAND: Windham Co., Weatherby and Upham #6910 (GH); Kent Co., Beattie s.n. (US); Providence Co., Collins s.n. (GH); Washington Co., Batchelder #4098 (USF); Newport Co., Mearns #506 (US).

9. Heterotheca flexuosa (Nash) Harms, Castanea 34: 408. 1969.

Chrysopsis flexuosa Nash, Bull. Torr. Bot. Club 23: 107. 1896.

Pityopsis flexuosa (Nash) Small, Man. S.E. Fl., 1341. 1933.

Perennial, short rhizomes from woody rootstock. Stems ascending, 1-6 in number, 2-5 dm high, slender, 2.8 mm

wide at base, flexuose and zig-zag in appearance, normally not branched, moderately covered with long silky hairs which are deciduous with age, stem purple tinged. Basal leaves similar to cauline leaves, absent usually at flowering time, overwintering. Cauline leaves covered with long silky hair, glabrate with age, upperside with strigose hairs intermixed, spreading-erect, slightly falcate; lower leaves 3-7 mm wide and 2.8-7 cm long, oblanceolate, acute, sessile; upper leaves somewhat reduced in size 3-5 mm wide and 1.9-5 cm long, usually linear to lanceolate, acuminate, sessile. Inflorescence cymose with few heads (3-20) per stem, peduncles arising from upper nodes of stems, 1-2 heads per peduncle. Peduncles varying in length from 1-11 cm, 0.5-1.0 mm in thickness, tomentose hairs also few light colored glands; few minute, peduncular bracts. Heads few (3-20) per stem, involucres 5-7 mm wide and 7-11 mm high, turbinate to campanulate. Phyllaries imbricate in 4-6 series, scarious, center herbaceous, pubescence silky; no glands; outer narrow, linear 0.6-0.8 mm wide and 2-3 mm long; inner 0.7-1.0 mm wide and 6-8.5 mm long linear-lanceolate. Disc corollas 25-45 in number, 5.5-7 mm long, slightly pilose, lobes 0.5 mm long. Ligulate corollas 9-13 in number; limb 5-8 mm long. Pappus double; outer of 14-27 setiform squamellae 0.3-1.0 mm long; inner of 30-50 barbellate capillary bristles. Achenes fusiform with

obscure ribs, slightly sericeous. N=9.

Flowering time: August to early October mainly.

Type: Nash #2545, in the pine lands of Bellair, Leon Co., Florida, about 4 miles south of Tallahassee, September 3, 1895. (NY!, Isotypes F, GH, MO, US) (Figure 26).

Variation and ecology: Only a limited number of specimens of H. flexuosa were studied (39) along with one population sample. This entity is clearly separate from the nearest related species (H. pinifolia and H. falcata). In appearance only H. falcata might be confused with it. However, the undulate leaf surface, very pronounced zig-zag stem, wider non-conduplicate leaves, and longer involucral height would differentiate it from H. falcata.

The chromosome number is N=9, and no meiotic irregularities were seen.

H. flexuosa is a limited endemic. Table VIII, page 56, indicates habitats as sandy (63 percent), oak (21 percent), and pine or pine-oak (28 percent). The soil types apparently are Red-yellow Podzolic. Apparently this is an area of limited endemics Gentiana pennelliana (Pringle, 1967), Torreya taxifolia, Taxus floridana, Phoebanthis grandiflora and others (James, 1961). No distinctive habitat was seen when field studies were made. Several of the species in section Pityopsis (H. graminifolia,

Figure 26. Type specimen of Heterotheca flexuosa (Nash) Harms.

H. microcephala, H. adenolepis, H. aspera, and H. flexuosa) are found in similar or the same habitats.

Distribution: Found only in four counties around Tallahassee, Florida (Figure 23, page 151).

Representative specimens: A total of 39 herbarium specimens were seen along with one population sample. The following are the only specimens seen: FLORIDA: No county, Rugel #485 (GH, US, MO, F, NY); Gadsden Co., (GH, NY); Leon Co., Bowers #70-484 (TENN), Clewell #501 (NCU), Clewell #743 (LSU, NCU), Godfrey #52502 (FSU, DUKE), Godfrey #58844 (FSU), Godfrey #55218 (SMU, GH, USF, FSU, NY, GA), Harper and Wehmeyer s.n. (MICH, NCU), Luzor #5132 (FSU), McDaniel #3675 (FSU, VDB), Morrill #1922 (NCU), Nash #2545 (US, GH, MO, F), Redfearn #404-14-55 (GA); Liberty Co., Godfrey #60235 (SMU, FSU); Wakulla Co., Godfrey #70072 (FSU, DUKE, VDB, NCU, TEX), McDaniel #3679 (FSU, VDB).

10. Heterotheca pinifolia (Ell.) Ahles, J. Elisha Mit. Sci. Soc. 80: 172-173. 1964.

Chrysopsis pinifolia Ell., Sk. Bot. S.C., and Ga. 2: 355. 1824.

Pityopsis pinifolia (Ell.) Nutt., Trans Am. Philos. Soc., s.2, 7: 318. 1841.

Diplogon pinifolium (Ell.) Kuntze, Rev. Gen. 2: 334. 1891.

Perennial, rhizomatous with short and longer rhizomes

to 15 cm or longer. Stems erect, 2-5 dm high, slender, arising from basal rosette of leaves, branched above middle, glabrous except for minute light colored hairs (tomentose?), stem somewhat purplish, striate. Basal leaves, shorter than cauline leaves (1-4 cm long) but broader 2-4 mm wide, sessile, linear, acute, mucronate, villous both sides but especially along margin of leaves. Cauline leaves olive-green, numerous and crowded, spreading to erect; lower leaves somewhat pubescent but glabrate with age, linear-filiform, acuminate, 0.8-1.4 mm wide and 3-7 cm long; upper leaves 0.4-1.0 mm wide and 1.8-6 cm long, filiform, mucronate, almost glabrous. Inflorescence cymosely paniculate, few to many branches, 2-8 heads per branch. Peduncles arising from upper nodes, 1-4 cm long, minutely puberulent, few bracteoles (0-4). Heads campanulate to turbinate, 5-7 mm wide and 5.5-8 mm high. Phyllaries imbricate in 5-6 series, imbricate, scarious except for herbaceous center, glabrate except few light colored glands, fimbriate apex, strongly keeled; outer 1.0-2.4 mm long and 0.4-0.7 mm wide; inner 4.8-6 mm long and 0.8-1.0 mm wide. Disc corollas 15-35 in number, 4.8-6.5 mm long, lobes 0.5 mm long. Ligulate corollas 9-13 in number; limb 5-7 mm long. Pappus double; outer of 14-25 setiform squamellae 0.6-0.9 mm long; inner of 30-40 barbellate capillary bristles 4.5-6 mm long. Achenes fusiform, 4 mm long,

inconspicuous ribs, sericeous. N=9.

Flowering time: August to early November.

Type: Apparently no specimen has survived in the Elliott Herbarium (now housed at the Charleston Museum, South Carolina) or none were listed by Weatherby (1942), and the Museum director (personal correspondence) indicated that he knew of no such specimen also. Dress (1953) indicated in his dissertation that a specimen in the New York Botanical Museum (NY) was inscribed "from Mr. Elliott." This specimen is marked in ink "Chrysopsis n. s." and in pencil "Alab. Elliott." Dress designated this as a neotype at the time, but it was not published. Since no other known Elliott specimen apparently exists, this is probably an acceptable choice. (Representative specimen Figure 27).

Variation and ecology: Heterotheca pinifolia is distinct because of its (1) narrow filiform to linear-filiform cauline leaves, (2) almost glabrous stems, (3) non-glandular peduncles, and (4) stems arising from short rhizomes. This species is distinct and fairly uniform except for slightly broader leaves in the Taylor County, Georgia specimens.

None of the other species could very easily be confused with H. pinifolia. The diploid chromosome number is N=9, and no meiotic irregularities were seen.

Only one natural hybrid was found in this group (H.

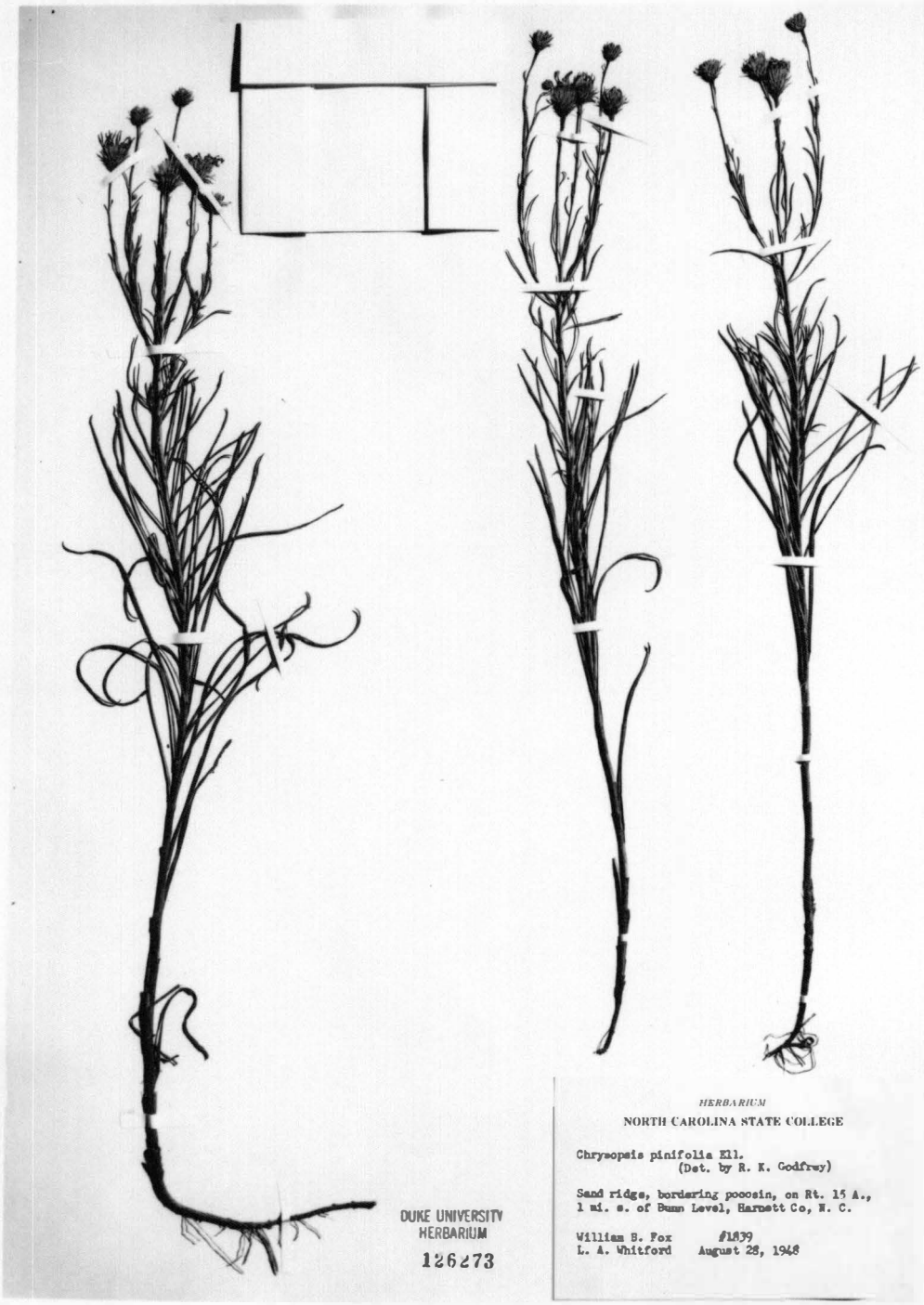
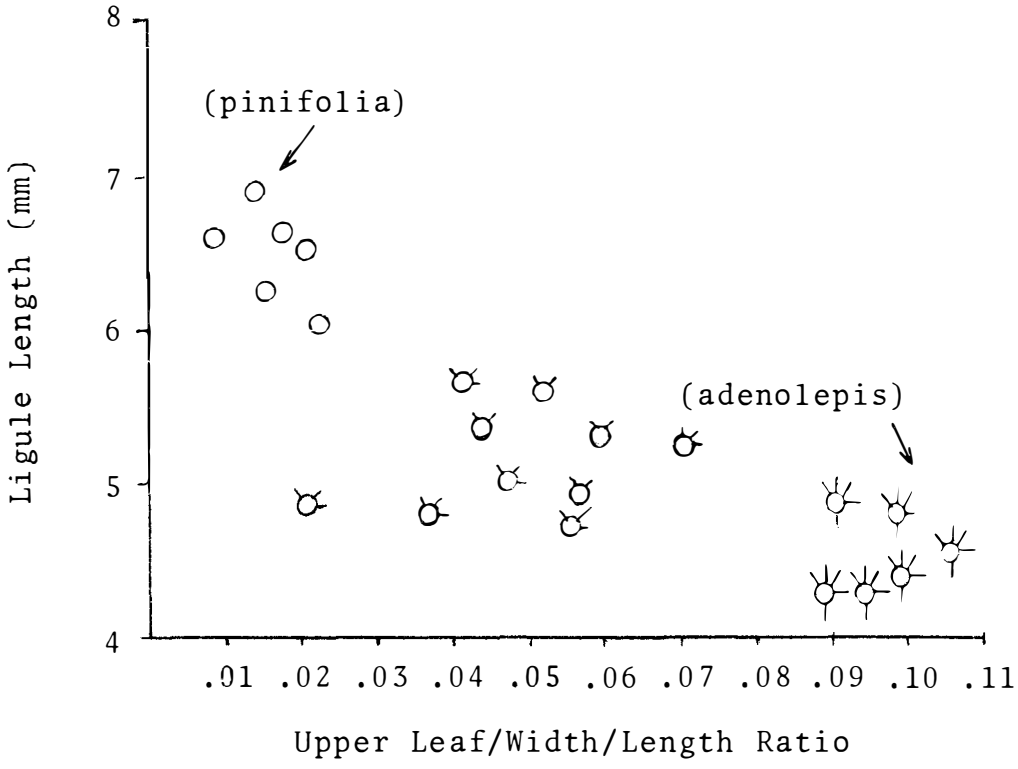


Figure 27. Representative specimens of Heterotheca pinifolia (Ell.) Ahles.

adenolepis with H. pinifolia). No other herbarium specimens seen appeared to be hybrids. This hybrid area in Moore Co., North Carolina, in which hybrids occur was in the sandhills in an eroded waste area. A number of plants were sampled. The soil was sandy, dry, and sterile. The hybrids show intermediate characters between the parents, which include leaf width/length ratio, ligule length, pubescence of phyllary, stem, and leaves, and glandularity of peduncle and phyllaries (Figure 28).

The parents (H. pinifolia and H. adenolepis) showed pollen stainability ranges above 90 percent; however, the hybrids range from 20.1 percent to 72.4 percent stainability. Apparently some backcrossing with parents has taken place. The cytological analysis of the F_1 hybrids showed regular pairing at metaphase I.

Heterotheca pinifolia is limited to the fall-line sandhills of North Carolina, South Carolina, and Georgia (Figure 21, page 137) and contributes significantly to the flora in August and September. This area is in the Norfolk soil group and Orangeburg soil group (Duke, 1961) which are droughty, rather sterile, sandy soils. This area has a distinctive vegetational type (Duke, 1961) where flowering is in the late summer as is true of H. pinifolia. This could be because normal fall rains would be enough to provide the young seedlings with moisture until their roots



Peduncle-glabrous

Peduncle-glandular

Phyllaries-sparse to glabrate

Phyllaries-intermediate

Phyllaries-glandular

Phyllary-glabrate

Phyllary-pubescent

Leaf-glabrate

Leaf-intermediate

Leaf-sericeous

Stem-sparse

Stem-intermediate

Stem-pubescent

Figure 28. Population sample analysis of a hybrid swarm between Heterotheca adenolepis (N=9) and Heterotheca pinifolia (N=9) located in Moore County, North Carolina.

could reach the deeper moister soils. For as Wells and Shunk (1931) indicated:

> Under a low nutrient condition which inhibits growth, only those plants survive which restrict water outgo, since in the sand, the roots with inhabited growth may reach only a limited amount of water. . . . In connection with the sterility problem, attention may well be again directed to the concomitant factors of low bacterial count, low CO_2 evolution, low total N, and extremely high C/N ratio.

While three species of section Pityopsis are found in the sandhills (H. graminifolia, H. adenolepis, and H. pinifolia), H. pinifolia is probably the more abundant. In H. pinifolia the leaves are almost filiform which could serve functionally as a water-conserving factor. This area formerly was high in longleaf pine composition (Wells and Shunk, 1931), but intensive cutting has reduced this in a number of areas and second growth oak or oak-pine is prevalent. In Table VIII, page 56, habitats indicated are sand (73 percent), open areas (10 percent), and woodsides (21 percent). It is in some areas a weedy invader after fields are abandoned and, in fact, Duke (1961) thought it was a recent invader of North Carolina.

Distribution: Found only in Taylor County, Georgia, and a few counties in North Carolina and one in South Carolina in the sandhill regions.

Representative specimens: A total of 64 herbarium specimens were seen along with two populations samples.

The following are all specimens seen: GEORGIA: Taylor Co., Bowers and Wofford #72-562a (TENN), Dress #2645 (FSU, NY), Harper #2238 (F, MO, GH, US, NY), Harper #1802 (F, NY, GH, US, MO).

NORTH CAROLINA: Harnett Co., Fox and Whiteford #1839 (DUKE, GA, FSU, GH, SMU), Radford #45276 (NCU, LAF, USF, TEX), Duke #Q-3375 (NCU), Stewart s.n. (NCU); Moore Co., Bowers #70-110 (TENN), Godfrey #50115 (PH, FSU, NCU, DUKE, KANU, US, NY, TEX, SMU), Henry #5683 (PH), Schallert s.n. (CU, SMU, NY), Freeman #56773 (NCU), Duke #Q-3369 (NCU), Duke #2517 (NCU), Schallert s.n. (NY); Richmond Co., Duke #2481 (NCU, FSU); Scotland Co., Gupton #1685 (NCU); Wayne Co., Duke #2622 (NCU), Radford #31568 (NCU), Godfrey, Fox, and Boyce #50634 (FSU, DUKE, GH, MO, SMU, NY), Radford #31548 (VDB, GA, FSU, NCU, SMU, NY).

SOUTH CAROLINA: Lexington Co., Ahles #53507 (NCU), Radford #29820 (KANU, NCU), Elliott s.n. (NY).

CHAPTER VII

SUMMARY

A biosystematic study of the section Pityopsis of the genus Heterotheca was undertaken. Cytological, morphological, chromatographic, and hybridization studies were utilized to provide a basis for taxonomic treatment of the taxa involved. Based upon the studies and the results obtained, it was decided that the taxa in section Pityopsis should best be treated as nine species, one with two varieties (one of which is new). The species could be divided into two broad groups; the Heterotheca graminifolia group (H. adenolepis, H. aspera, H. graminifolia, H. microcephala var. microcephala, and var. aequilifolia, and H. oligantha) and the H. pinifolia group (H. falcata, H. flexuosa, H. pinifolia, and H. ruthii). Heterotheca ruthii appears to be intermediate between the two groups and is closely related to H. oligantha.

Cytology indicates the diploid species (N=9) are in the majority with only H. adenolepis (both diploids and tetraploids), H. graminifolia, and H. oligantha being tetraploids (N=18). In almost all cases normal meiotic pairing occurred. Pollen measurements indicated a significant difference between the two tetraploids, H. oligantha and H. graminifolia and the diploid species. No significant

difference was found between the two chromosomal races of H. adenolepis.

The paper chromatographs were somewhat inconclusive but in general followed the other taxonomic evidence for the section. Heterotheca pinifolia was shown by the chromatographs to be more closely related to the H. graminifolia group than can be demonstrated by using other evidence.

Heterotheca adenolepis, H. aspera, H. microcephala (both varieties) appear to be closely related, and it is thought that H. adenolepis was derived via hybridization between H. aspera and H. microcephala var. microcephala. The latter two are thought to be among the more primitive in the section along with H. graminifolia and H. ruthii. Heterotheca graminifolia was thought to have been derived via autopolyploidy from H. microcephala. These last two are widespread in the Coastal Plain. Heterotheca oligantha is of unknown origin but appears closely related to H. ruthii and H. graminifolia.

Heterotheca pinifolia, H. falcata, H. flexuosa, and H. ruthii apparently were derived from one or more primitive ancestors which migrated from an Appalachian center of origin to the Coastal Plain, became geographically separated and evolved into the four entities listed above. Heterotheca ruthii appears to be the most primitive of the four species. All are relatively limited in range with H. ruthii found in

the Hiwassee Gorge in East Tennessee; H. flexuosa in a few counties in Florida; H. pinifolia in a few counties in the Sand Hills of Georgia and North and South Carolina; and H. falcata in sand areas in five northeastern states (Connecticut, Massachusetts, New Jersey, New York, and Rhode Island).

Hybridization experiments have shown relatively few barriers between geographically widely separated species such as H. pinifolia, H. ruthii, and H. flexuosa. Some cytological barriers appear to be present in southern Coastal Plain species which overlap in that area such as H. adenolepis, H. graminifolia, H. aspera, and the two varieties of H. microcephala. In more northern areas, however, such as in North Carolina and Virginia, introgression apparently does take place between H. graminifolia and H. adenolepis.

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APPENDIX

APPENDIX A

DATA SHEET USED IN STUDY OF HETEROTHECA SECTION PITYOPSIS

Annotation

Rhizomatous

Stem height

Stem diameter

Lateral branches

Lateral branches no.
Lateral branches length

Basal leaf width length

Lower cauline leaf width length

Upper cauline leaf width length

Leaf pubescence

Peduncle length dia.

Involucral dia. height

Phyllary no.

Outer phyllary length width

Inner phyllary length width

Integrating with bracteoles yes no.

Bracteole number

Phyllary pub. or flandularity

Disc corolla tube length

Ligule length

Stigmatic surface
pilose length

pappillae length

Anther length

Anther width

Pollen via.

Pollen non-via.

	Range	Avg.
Pollen size w/spines		
Pollen size (inside)		

Chromosome N=

Head number flower no.
disc ray

Achene length

Outer pappus length no.
Inner pappus length no.

State Co. Col:

Habitat No.

Heterotheca

VITA

Frank D. Bowers was born in Fayetteville, Arkansas, on March 21, 1936. He spent most of his early years in Kansas City, Missouri, and was graduated from East High School in 1954. Frank entered Southwest Missouri State College in Springfield, Missouri, in 1962, and graduated from that institution in 1966 with a B.S. in Conservation Education. He entered The University of Tennessee, Knoxville, under a NSF Traineeship in the fall of 1966 and obtained his M.S. degree in 1968 in Botany. He then obtained a position as Assistant Director of the Herbarium from 1968 to 1970 at The University of Tennessee. Returning as a full-time student in 1970, he expects to obtain his Ph.D. from that institution in December of 1972. Frank is married to a UT graduate, Donna Olsen Bowers.