This is to certify that the

thesis entitled

Taxonomic Implications of Distribution, Breeding Systems, Vestiture Type, and Pollen Morphology in Selected Mexican *Hieracium* Species

presented by

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has been accepted towards fulfillment
of the requirements for

Masters of Science degree in Botany

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Major professor

Date 13 July 1988

O-7639

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TAXONOMIC IMPLICATIONS OF DISTRIBUTION, BREEDING SYSTEMS, VESTITURE TYPE, AND POLLEN MORPHOLOGY IN SELECTED MEXICAN *HIERACIUM* SPECIES (COMPOSITAE)

By

Jacqueline Anne Soule

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Botany and Plant Pathology

1988

ABSTRACT

TAXONOMIC IMPLICATIONS OF DISTRIBUTION, BREEDING SYSTEMS, VESTITURE TYPE, AND POLLEN MORPHOLOGY IN SELECTED MEXICAN *HIERACIUM* SPECIES (COMPOSITAE)

By

Jacqueline Anne Soule

The taxonomic relationships of the polytypic Mexican Hawkweeds, *Hieracium abscissum* Less., *H. dysonymum* Blake, *H. mexicanum* Less., *H. pringlei* A. Gray, *H. schultzii* Fries, and two potentially new taxa, *H. 'potosi'* and *H. 'chipinque'* were addressed in this paper. Extensive field work discovered no clearly intermediate or hybrid individuals, indicating that the polytypy observed in herbarium specimens is more likely due to responses to different sites than to hybridization. Breeding system studies which included pollinator exclusion in-situ, emasculation, and artificial selfing indicate that these *Hieracium* species are outcrossers. A vestiture survey based on scanning electron microscopy (SEM) and analysis by Spearman's Rank Correlation and Average Linkage Cluster Analysis resulted in the taxa sorting into two groups, the *Hieracium abscissum-schultzii* group to which *H. 'chipinque'* belongs, and the *Hieracium dysonymum-mexicanum* group to which *H. 'potosi'* belongs. SEM studies of pollen morphology determined two groups which correspond to the plants' growth form. The many headed species -- *Hieracium abscissum*, *H. schultzii*, and *H. 'chipinque,'* have curved spines; the few headed species -- *H. dysonymum*, *H. mexicanum*, *H. pringlei* and *H. 'potosi,'* have straight spines. The number of annular and lacunar pollen spines provides evidence for not recognizing *Hieracium 'chipinque'* and *H. 'potosi'* as separate taxa since these pollen characters agree with other characters, particularly vestiture, of *H. abscissum* and *H. dysonymum* respectively.

DEDICATION

To the people whose love, encouragement, and belief in me made this dream a reality; my grandfather and grandmother, my father, my brother, and my mentor.

ACKNOWLEDGMENTS

I wish to express my gratitude to all those who provided guidance, help, and support during this study. My thanks especially to Dr. John H. Beaman, my major professor, for his efforts, and to my committee members, Dr. Karen Klomparens and Dr. Stephen Stephenson for their invaluable input. I am also indebted to Dr. Peter Murphy who provided me with space for growing plants. Technical assistance was freely given by the members of Dr. Chris Stevens', and Dr. Barbara Sears' labs and by the staff at the Center for Electron Optics, for which I thank them all.

Of course, none of this would have been possible without the people who helped me find my way, and all the people at MSU who became my friends and gave me the support, encouragement, spelling corrections, and suitable libations as the occasion warranted. I thank them all and list them below in no particular order: Jeremy Soule, Cynthia Baker, Thomas Harland III, Graham Smart, Sara Kaplan, Koibeatu, Gerald 'Stinger' Guala, Tom Trana, Shirley Owens, Chris Pedersen, Tracy Wacker, Carolyn Pazur, Phil Jensen, Peggy Hogan, Tom Isakiet, Barry Stein, Kate Everts, and the attendees of the Plant Diversity Discussion Group and the Alex B. Filanow Memorial Symposium.

Collecting expeditions to Mexico were made possible in part by funds from the William T. Gillis Memorial Fund and an award from the Michigan State University Chapter of the Society of The Sigma Xi.

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INTRODUCTION

The genus Hieracium (Compositae, tribe Lactuceae) includes herbaceous perennial species found in boreal and temperate regions of Europe, Asia, North and South America. The generic epithet comes from the Greek hierax: a hawk, and comes to us from "...the ancients as recorded by Pliny and others, supposing that the hawks used the plant to strengthen their eyesight" (Fernald 1950). The common name is Hawkweed.

Over the years Hieracium has gained notoriety for being one of the most taxonomically difficult of all genera. In the European species, polyploidy, apomixis and hybridization have been shown to be the major factors contributing to the biological complexity of the genus and have led to a proliferation of recognized species. As Gleason (1952) states, there are "...nearly 10,000 described species...of which perhaps only 200-300 should be maintained".

The last published revision on the genus in Mexico is that of Robinson and Greenman (1904). In a study of the genus in Mexico and Central America, Beaman (unpublished) has determined that there are approximately 18 species in that area. Six species need further work before a definitive statement about the taxonomy of the genus in Mexico and Central America can be made.

This study was limited to the problematical species found in eastern and central Mexico that have shown the greatest polytypy, *Hieracium abscissum* Less., *H. dysonymum* Blake, *H. mexicanum* Less., *H. pringlei* A. Gray, and *H. schultzii* Fries. These species are all widespread, and putative hybrids involving all of them were suspected on the basis of herbarium specimens. Two areas in particular had plants that were hard to definitively place to species. These areas represented potential northward extensions of range for known species or else sites of new species. This study also addressed the issue of affiliation for the plants from Chipinque Mesa, above Monterrey, Nuevo León, and Cerro Potosí, Nuevo León. These plants are referred to as *Hieracium* '*chipinque*' and *H.* '*potosi*.'

Little experimental work has been done on the Mexican species. Chromosome counts have been reported by Beaman and other workers, and the numbers are only diploid with $n = 9$. Thus, the complex variation may involve hybridization or inbreeding rather than polyploidy. Conversely, it might be due to ecotypical variation or adaptive radiation.

Four approaches to the problem were utilized: evaluation of geographic distribution patterns, breeding system studies, examination of the vestiture, and pollen analysis. Field work was conducted to search for range extensions, determine dispersion within a habitat, and evaluate localities where two or more *Hieracium* species grow together. The breeding system studies involved field work and hybridization of field-collected plants. The vestiture was examined by scanning electron microscopy (SEM) and the data statistically analyzed by two techniques. The pollen analysis utilized SEM on mostly field-collected pollen.

DISTRIBUTION, ECOLOGY, AND GEOLOGY

Introduction

Hieracium is primarily a temperate region genus that generally does not tolerate aridity, and thus in Mexico is found mostly in the highlands. These highlands range between 1,300 to 4,000 meters elevation, and are generally covered with pine-oak or pine forests (Miranda and Sharp 1950, Rzedowski 1978). Collections of the taxa addressed in this work show them to be found mostly in the northern Sierra Madre Oriental, the trans-Mexican volcanic range, and the Sierra Madre del Sur in Oaxaca and Chiapas. When label data were accumulated for preliminary location maps, the genus appeared disjunct, centering mostly around cities with universities or in highly accessible scenic areas. The separate collections of R. McVaugh, P. S. Martin, and J. H. Beaman from remote areas indicated that the species might have continuous ranges rather than disjunct ones.

Some species of *Hieracium*, however, are known to be disjunct, notably *H. mexicanum* which is only found at higher elevations, frequently above timberline, in the trans-Mexican volcanic range and south. *Hieracium abscissum*, *H. dysonymum*, and *H. schultzii* are found in slightly lower elevation moist pine-oak woods, although *H. dysonymum* has also been collected above timberline. *Hieracium pringlei* seems the most tolerant of aridity and is found at the lowest elevations, often in fairly xeric oak forests.

The two potentially new taxa, *Hieracium* '*potosi*' and *H*. '*chipinque*' are known only from single local areas. The parent material for the soil in both these areas is limestone (Beaman and Andresen 1966; B. L. Turner, personal communication). In most other areas in Mexico where *Hieracium* is found the soil is of volcanic origin (Beaman 1962, 1965; Jardel 1986; Flores 1985). It was suspected that *Hieracium* '*potosi*' and *H*. '*chipinque*' were endemic to limestone, edaphic endemism being common in many species (McVaugh 1943, 1952; Kruckeberg 1951, 1969; Braun 1955). *Hieracium pringlei* has been collected on limestone outcrops as well as from volcanic areas. Further collections of *Hieracium* '*potosi*' and *H*. '*chipinque*' were needed to determine if they were limestone endemic species, or whether, like *H*. *pringlei*, they represent known species which occur on various soil types.

The work of Clausen, Keck, and Hiesey (1941) demonstrates how greatly a taxon can vary based on the site to which it has adapted. Their demonstration of variations between populations based on topography indicates how careful systematists must be when recognizing new taxa. Ecological studies have been demonstrated to be useful in plant systematics, and were discussed at length by Kruckeberg (1969A). He indicates that extensive collecting with great attention to detail, such as soils and cover, can provide valuable ecological information on a group and eliminate problems of topographic variants. Field work was undertaken in part to determine the ranges of the species and to fill in the gaps in range maps, or to demonstrate the disjunction of the ranges.

An additional study was done to determine the type of dispersion within habitat and to see if it would shed light on the biology of Hieracium.

Methods

Specimens of Mexican Hieracium species were examined at the following herbaria: ARIZ, ASUA, MEXU, MICH, MSC, MO, TEX, and XAL (abbreviations after Holmgren et al. 1981). Also viewed were a large number of specimens from WIS that were on loan to Dr. J. Beaman, as well as his collections which have not yet been distributed. All label data were recorded from these specimens, in part to establish what sites had been collected, to determine where the species showed the greatest polytypy, and for the formulation of location and distribution maps (Figures 1 through 5). Location maps were compiled based on the information on herbarium labels. These maps were taken into the field and gaps between locations were extensively searched for the presence of any of the species. Sites where two or more of the polytypic species occurred were especially searched for. Distribution maps were compiled once all field work was completed and include the author's collections. Voucher specimens are in the Beal-Darlington Herbarium, Michigan State University (MSC).

Two field trips to Mexico were made. In 1986 approximately 50 sites were examined in likely habitats in the trans-Mexican volcanic belt. Prior collection localities were searched and attempts made to find new localities. Eighteen sites were found to contain the genus and were thus considered "collection sites." Collection sites were evaluated for: dominant vegetation, possible plant associations, cover, exposure, and elevation. Herbarium specimens, seeds, and where possible, live plants were collected. Photographs of habitat and individuals were taken at each site when weather permitted.

In 1987 roughly 400 sites were searched in likely-looking habitats throughout the Sierra Madre Oriental and the trans-Mexican volcanic belt. Fifty-three sites proved to contain the genus and are thus designated "collection sites." Collection sites in 1987 were evaluated for: slope (facing and degree), soil type, dominant vegetation, possible plant associations, cover, exposure, and elevation. Herbarium specimens, and where possible, live plants, pollen samples, and seeds were collected. Photographs of habitat and individuals were taken at each site when weather permitted.

Dispersion patterns within a locality were evaluated by line transect at five sites. The line transect was selected at a site once the first _Hieracium_ individuals were found. This was designated the starting point of a 100 meter transect. The transect was laid out by uncoiling a 100 m tape measure. Due to the nature of the habitats in which _Hieracium_ is found (steep mountain slopes, or often along the edges of cliffs or roadside cuts), a totally random direction for the transect could not be made. Instead, the worker faced up the slope and made the decision to run the transect to the left or right based on a coin toss; heads to the right, tails to the left. At the zero point and at each ten meter interval, a one meter square quadrat was established centered on the tape used to establish the transect. Within each of the 10 quadrats the number of individuals present and their age class was recorded. The three age classes were: 1) seedling (four or less leaves and small stature); 2) non-reproducing (more than four leaves and/or the size of a reproducing plant but lacking flower stalk); 3) reproducing.

Results and Discussion

The summer field work was successful in filling some of the gaps in the known distributions of Hieracium species in Mexico. The distribution maps (Figures 1 through 5) are compiled in part from the collections made by Soule et al. in 1986 and by Soule and Bodeau in 1987. The specimens of other collectors, particularly Beaman from 1957 to 1978, were also used. Specimens used for the maps are listed in Appendix I. These maps indicate that the northern Sierra Madre Oriental populations of Hieracium abscissum, and to a lesser degree H. dysonymum and H. schultzii, are disjunct from those in the trans-Mexican volcanic range. Hieracium pringlei has an almost continuous distribution; indeed, further collections in the states of San Luis Potosí and Durango may show this to be so.

Soils

Soil evaluation at each collection site indicates that Hieracium species are found on diverse soil types: H. abscissum, H. dysonymum, and H. schultzii were found growing in clay, rhyolitic, and volcanic ash soils; H. pringlei was found in limestone, gypsum, rhyolitic, clay, and

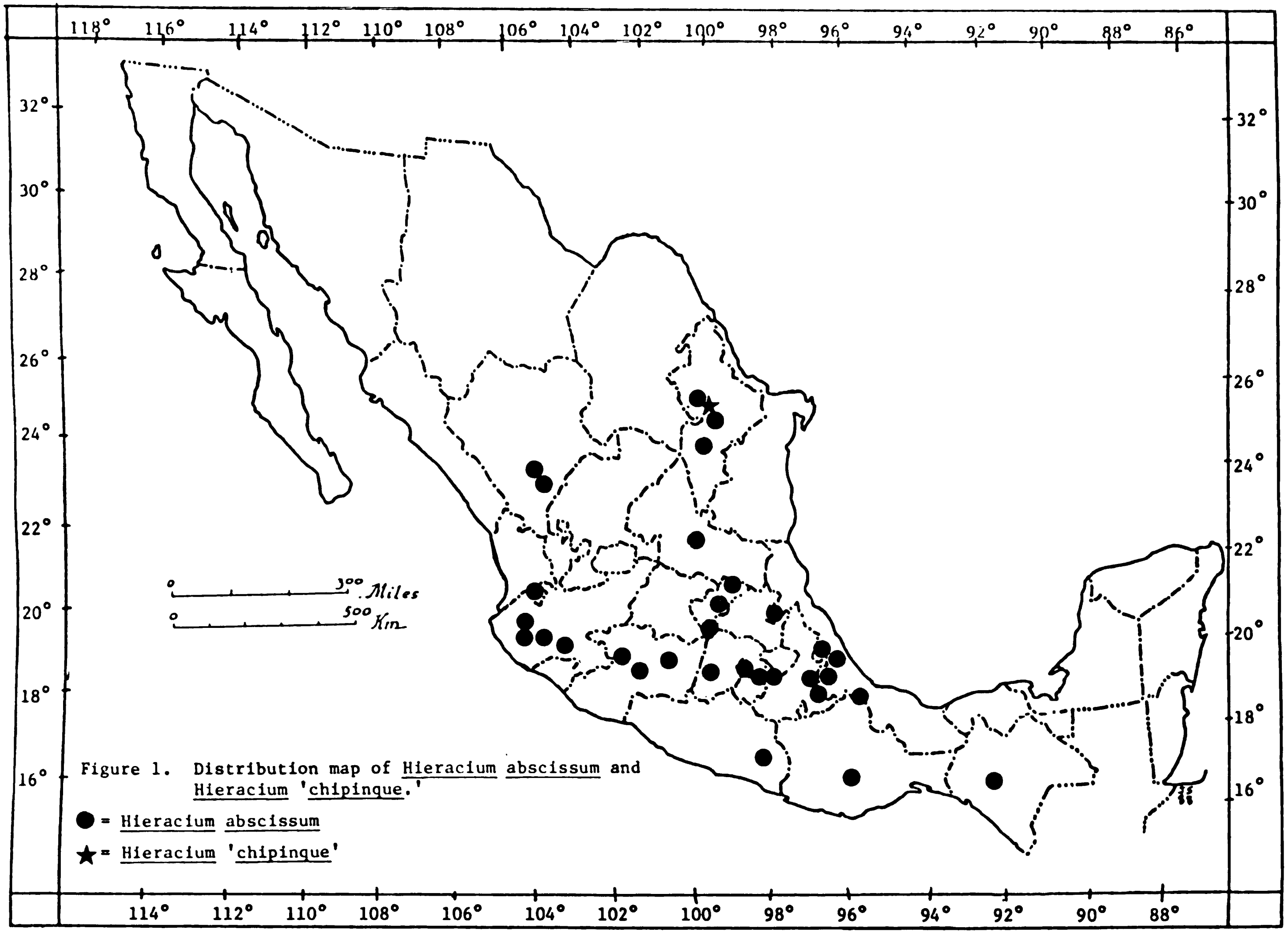

Figure 1. Distribution map of Hieracium abscissum and Hieracium 'chipinque.'

● = Hieracium abscissum

★ = Hieracium 'chipinque'

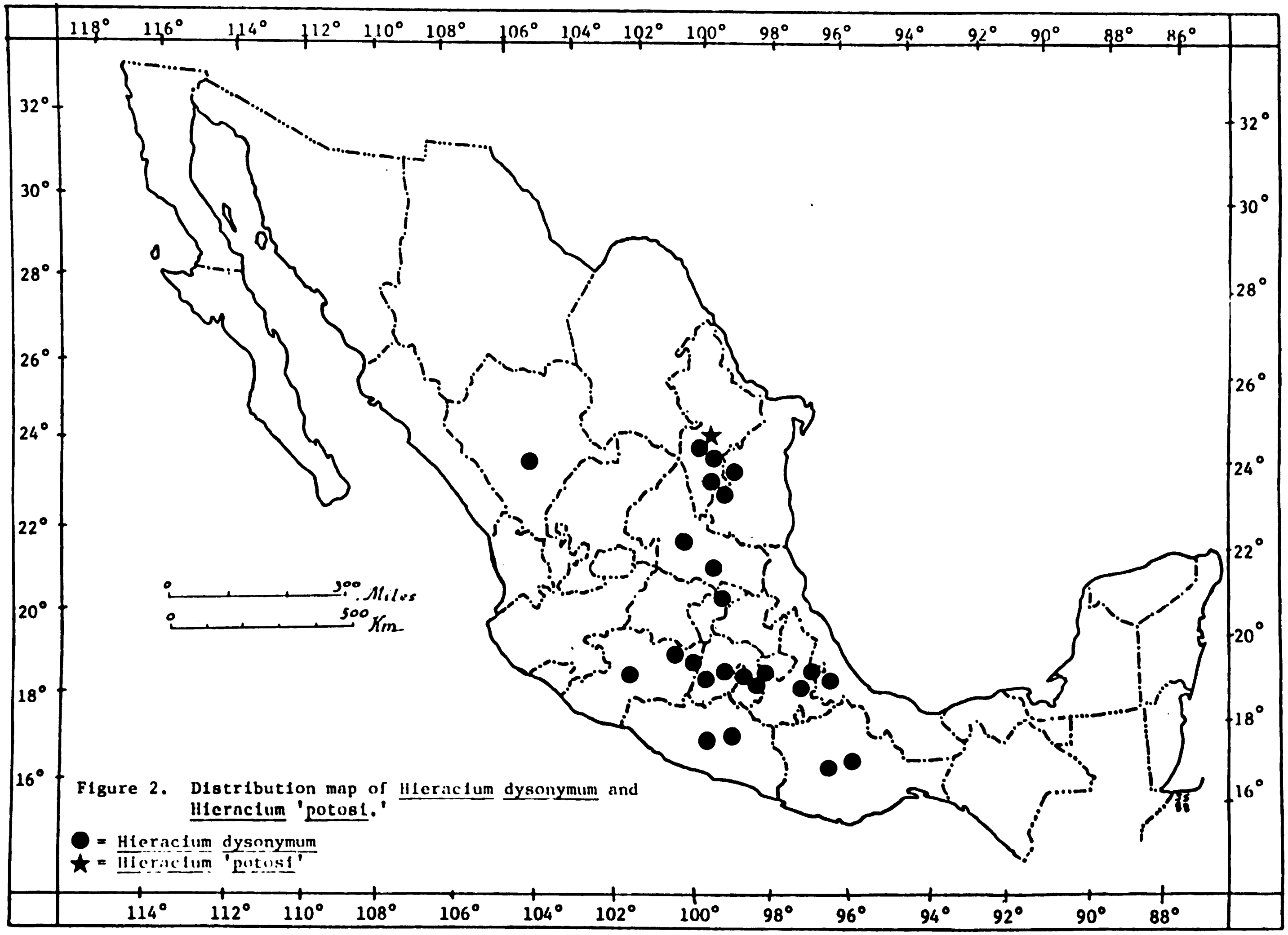

Figure 2. Distribution map of *Hieracium dysonymum* and *Hieracium 'potosi.'*

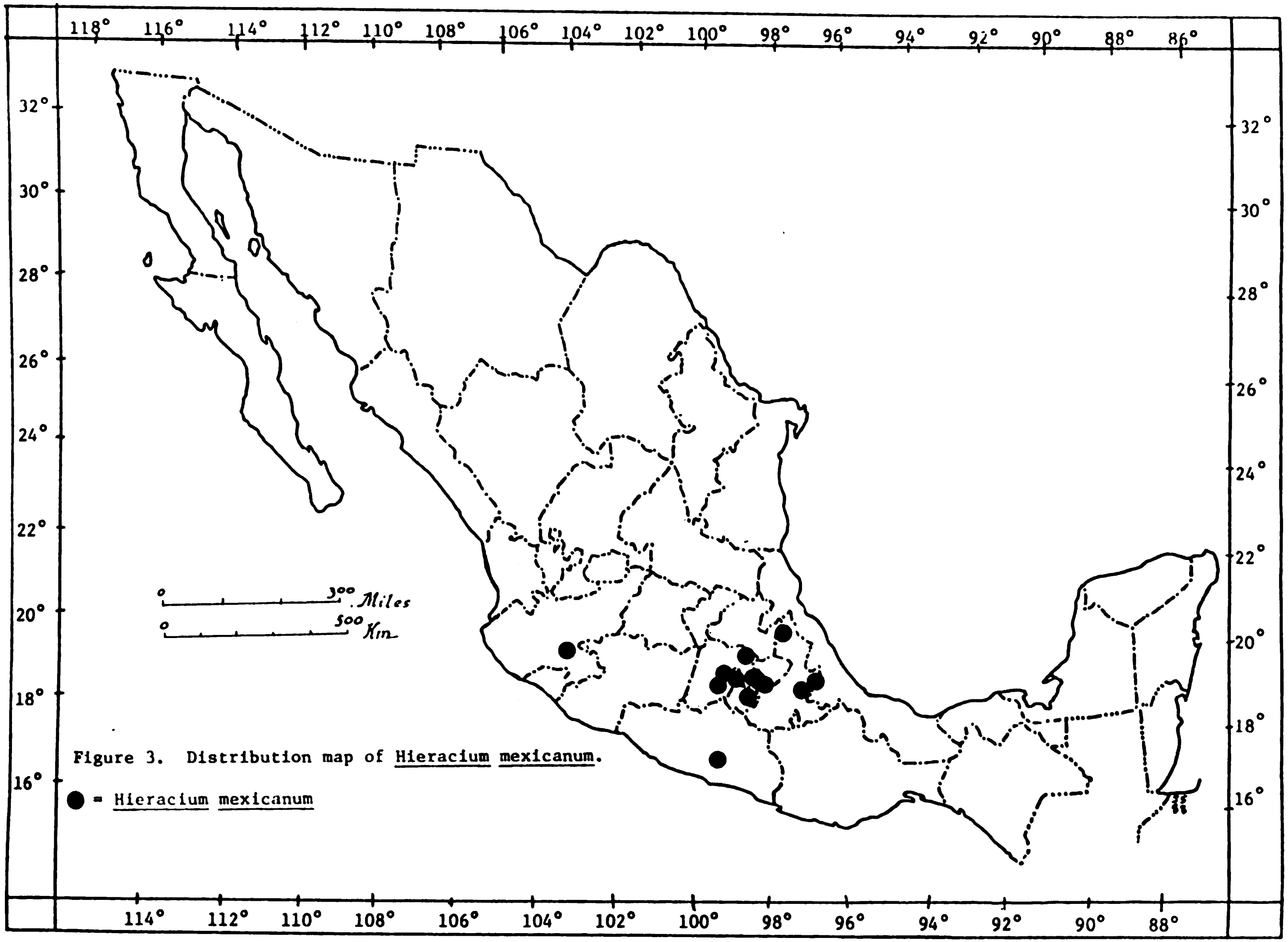

Figure 3. Distribution map of Hieracium mexicanum.

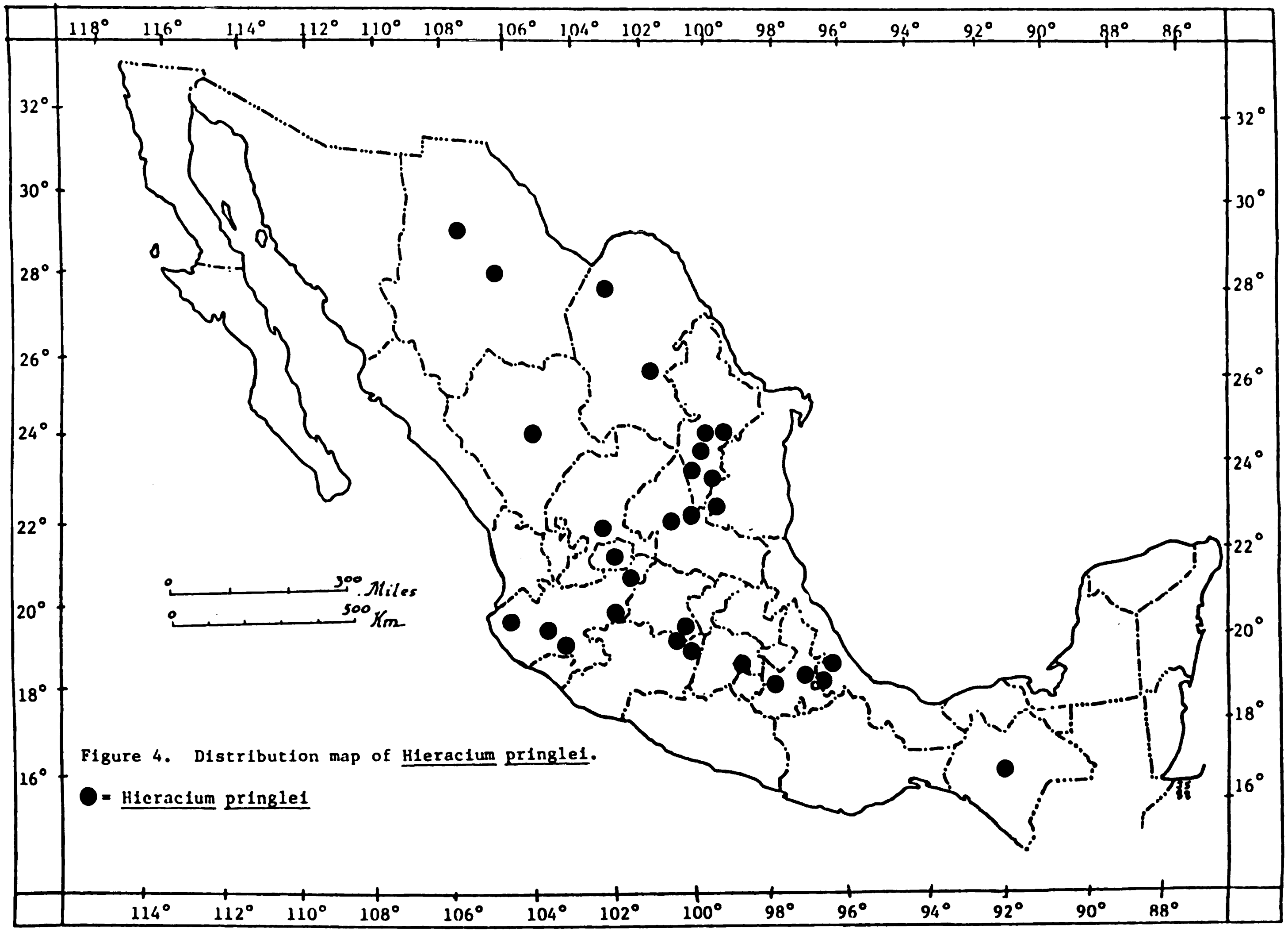

Figure 4. Distribution map of Hieracium pringlei.

● = Hieracium pringlei

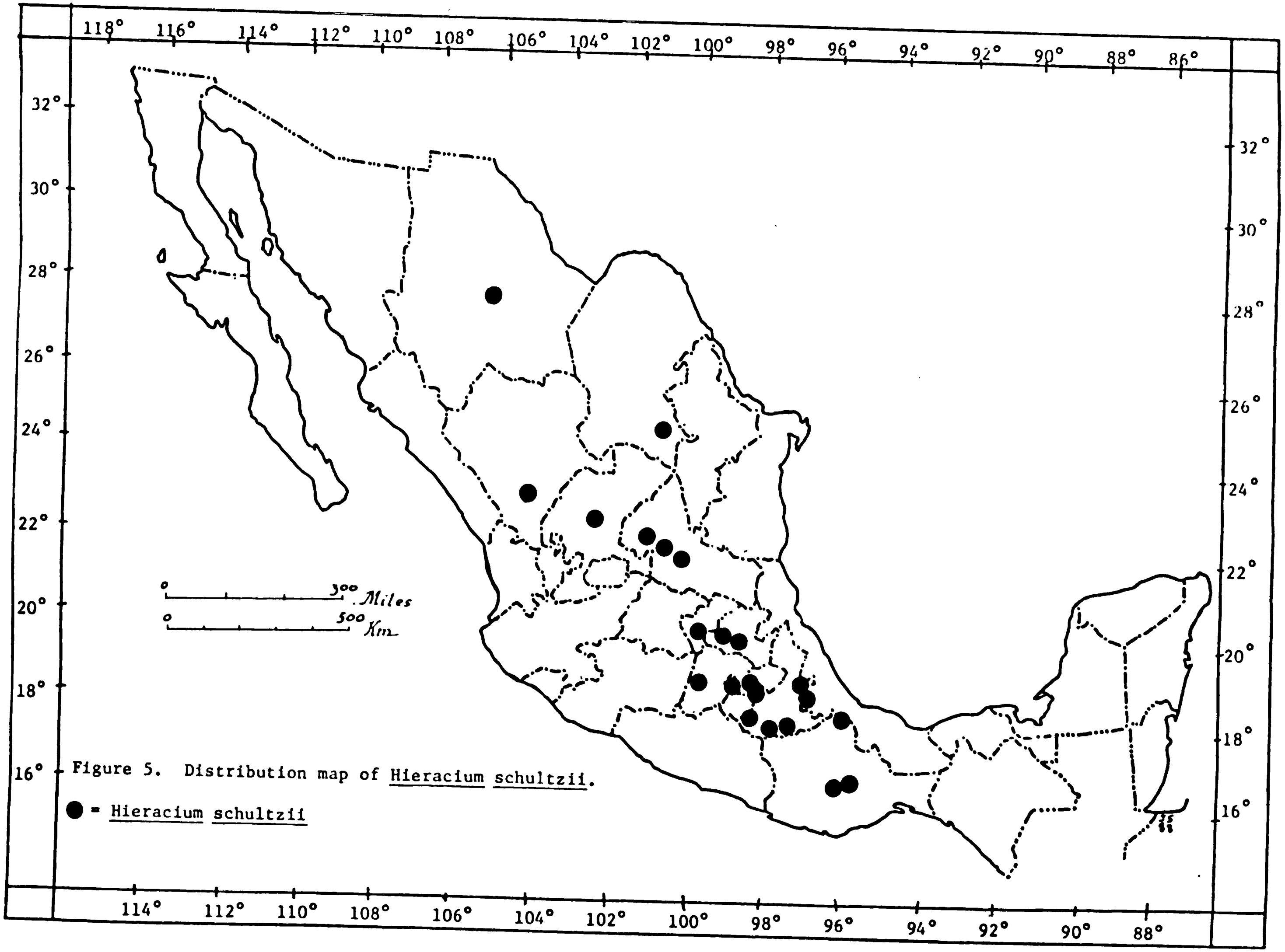

Figure 5. Distribution map of Hieracium schultzii.

● = Hieracium schultzii

Table 1. *Hieracium* taxa found growing together in the field and still differentiatable as to species.

	abs.	crep.	dys.	fend.	mex.	pring.	sch.	'chip.'	'pot.'
abscissum	---								
crepidispermum	YES	---							
dysonymum	YES	YES	---						
fendleri	YES	YES	YES	---					
mexicanum	YES	YES	YES	YES	---				
pringlei	YES	YES	YES	YES	NO	---			
schultzii	YES	YES	YES	YES	YES	YES	---		
'chipinque'	NO	NO	NO	NO	NO	NO	NO	---	
'potosi'	NO	YES	NO	NO	NO	NO	NO	NO	---

Table 2. Results of transects used to determine type of dispersion within a habitat.

Soule Coll. #	Age Class	Number of Individuals Present per Quadrat										Total #/ Age Class
		Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8	Q9	Q10	
1501	Reproducing	1	2	0	0	0	0	0	0	0	0	3
	Non-reproducing	4	0	0	0	0	0	0	0	0	0	4
	Seedlings	0	17	0	0	0	0	0	0	0	8	25
	Totals	5	19	0	0	0	0	0	0	0	8	32
1513	Reproducing	9	1	3	2	0	0	0	0	0	0	15
	Non-reproducing	25	0	1	5	0	0	0	0	0	0	31
	Seedlings	0	0	0	0	0	0	0	0	0	0	0
	Totals	34	1	4	7	0	0	0	0	0	0	46
1516	Reproducing	3	0	0	0	0	2	0	3	3	0	15
	Non-Reproducing	18	1	0	0	0	0	0	9	0	0	28
	Seedlings	2	0	0	0	0	0	0	3	0	0	5
	Totals	23	1	0	0	0	2	0	15	3	0	44
1593	Reproducing	11	0	0	0	0	0	0	0	0	0	11
	Non-Reproducing	27	4	0	0	0	0	0	0	0	0	31
	Seedlings	15	1	0	0	0	0	0	0	0	0	16
	Totals	51	5	0	0	0	0	0	0	0	0	56
1612	Reproducing	12	10	6	12	17	17	2	6	5	10	97
	Non-Reproducing	19	6	2	13	16	8	1	2	1	2	70
	Seedlings	5	4	1	4	4	4	2	2	3	5	34
	Totals	36	20	9	29	37	29	5	10	9	17	201

volcanic ash soils; *H. mexicanum* was found on volcanic ash and rhyolitic soils. *Hieracium 'chipinque'* and *H. 'potosi'* were extensively sought for in any place other than their known sites but no additional localities were found.

Naturally occurring hybrids

A significant aspect of the summer field work was the search for localities where species that are suspected of hybridizing were growing side by side, and were still distinguishable. Virtually every species of the polytypic group was found growing with every other species and yet could still be fairly easily identified (Table 1). At one site in Puebla, four different species were growing together and no hybrids were found. This does not say that hybridization does not occur, it simply indicates that conspicuous hybrid individuals or swarms were not observed. If gene flow is occurring between species, other techniques, such as gel electrophoresis, will be necessary to document the matter.

Dispersion within a habitat

The results of the dispersion study (Table 2) clearly indicate clumped occurence patterns. This seems to be due to two facts, underground structure and seed dispersal mechanisms. The *Hieracium* species investigated have a rhizomatous habit. Excavations of numerous plants showed that new shoots were produced at the base of the old plant once flowering had been completed. New shoots are produced along a central rhizome and generally grow 1 to 10 cm away from the central root prior to turning upward. While collecting live plants for breeding system studies, it was common to gather 3 to 10 interconnected individuals in a 10 cm square area.

Seed dispersal patterns also may lead to the clumped dispersion. While running the transect, several individuals categorized as "seedlings" were excavated and showed very tiny roots with no underground connection to other members of the community, indicating that they were indeed seedlings. In some cases these seedlings were growing adjacent to a flowering individual, or even under the leaves of mature plants. This indicates that some of the seed is not dispersed very far by wind, despite the pappus. Stergios (1976) found this pattern in Hieracium aurantiacum in Michigan, where most seed was deposited within 1 meter of the source. Another consideration is the fact that Hieracium species in Mexico are often on isolated mountains which can be likened to islands of suitable habitat, surrounded by harsh seas of arid or cultivated land. Shmida's (1985) work on Compositae with an inconsistently deciduous pappus indicates that this condition is of selective advantage in species that are found in habitat islands, although it is not limited to those species. These findings expand upon Carlquist's (1966A, 1966B, 1966C, 1967) work on seed dispersal habits of Pacific Island Compositae and other groups, in which he found many instances of island plants lacking the long distance seed dispersal mechanisms which originally enabled them to colonize the island.

Locations in general

Although the areas where Hieracium are found are for the most part not geologically recent (Jones 1976, Beaman and Andresen 1966, Beaman 1962, 1965; Martin and Harrell 1957, Dressler 1954, Sharp 1953), the sites are recent in some respects. The polytypic species are almost always found in disturbed sites. They were not found in the most recently disturbed situations; rather, they are a part of the wave of secondary colonizers, occurring in the partial shade found under young trees. This was amply illustrated by the search of the site of *Hieracium dysonymum* collected by Rogers McVaugh in 1949 (*McVaugh 9878*), a site in the state of Michoacán where they were reported as "abundant." Three hours of searching yielded one individual (*Soule 1393B*) in 1986. In a subsequent telephone conversation with Dr. McVaugh, he mentioned that the plants were all over the slopes under "recently planted pines." In 1987 the site was revisited with special attention paid to open areas at the edges of the dense forest. Numerous *H. dysonymum* were found (*Soule 1582*, *1583*).

Conclusions

Based on the fact that virtually every one of the species studied was found growing along side every other species, with no clearly intermediate individuals, it appears that hybridization may not be a major factor in influencing variation.

Field work determined that the northern Sierra Madre Oriental populations of *Hieracium abscissum*, and to a lesser degree *H. dysonymum* and *H. schultzii*, are disjunct from those in the trans-Mexican volcanic range. *Hieracium pringlei* has an almost continuous distribution.

Clumped dispersion and habitat preference indicate that the Mexican *Hieracium* species are secondary colonizers which have suitable sites for growth only for a short period of time prior to being forced to spread to new locations by the closing of the forest canopy.

BREEDING SYSTEM STUDIES

Introduction

Naturally occurring hybrids have long been a thorn in the side of the plant taxonomist (Wagner 1968; Baum 1969, 1971). Various types of studies have been done in an effort to clarify the question of hybridization in different groups as exemplified by the approaches of Bell (1952), and Turner and Alston (1959). Summaries of various approaches are found in the works of Constance (1964), Heiser (1963, 1966, 1969), and Turner (1964, 1967, 1969). One such approach is breeding system studies which generally involve culturing the suspected parental species and attempting to reproduce the hybrids (Jones 1966). Breeding system studies have been done on a group of western North American *Hieracium* species. Kruckeberg (1967) was able to cross two different species that are found in the Olympic Mountains in Washington. From these crosses he raised viable offspring, although the F_2 generation had reduced fecundity. Christy (1986) was able to cross three species of eastern North American *Hieracium* but only two of the crosses yielded viable offspring.

To determine if hybridization was a factor leading to the polytypy of the Mexican species, a series of hybridization studies was planned. Live plants were needed and they were obtained by field collection and by growing seed that was field collected.

Apomixis results in additional complex variation that affects plant classification (Stebbins 1950). Localized populations that are apomictic can vary slightly from other populations, resulting in a tendency for prolific naming of new species. European species of *Hieracium* are frequently apomictic and have fallen prey to rather zealous workers with "...eyesight stimulated beyond that of the ancient hawks...[resulting in]...thousands of so-called species, subspecies, varieties and forms..." (Fernald 1950).

Based on preliminary observations, Beaman (personal communication) suspected that some Mexican *Hieracium* species may be apomictic. Cytological work in *Hieracium* dates back to Sears in 1917. Cytological studies can prove polyploidy and apomixis as shown in the work on *Townsendia* by Beaman (1954, 1957), and more recently in the work on *Poa* by Kellogg (1987). Chromosome counts of Mexican species of *Hieracium* have been done by various workers and the counts found only diploids with n = 9 (Table 3). Other techniques used to determine apomicts in Compositae include pollinator exclusion and emasculation. Emasculation was done by Guppy (1978) in her work on British Columbian *Hieracium*. Pollinator exclusion studies are useful in that they can show whether the species is selfing and/or apomictic versus obligately outcrossing. Christy (1986) demonstrated the technique's usefulness in her work on three species of *Hieracium* in southeastern North America. Cytological evidence, emasculation of flower heads, and pollinator exclusion studies were utilized in this study.

Table 3. Chromosome counts of Mexican species of Hieracium.

Species	n Number	Reference
H. abscissum	9	McGregor 16584 (KANU), unpublished.
H. abscissum	9	Harms, 1973.
H. mexicanum	9	Beaman, DeJong, and Stoutamire, 1962.
H. mexicanum	9	Beaman and Turner, 1962.
H. pringlei	9	Keil, Luckow, and Pinkava, 1988.
H. pringlei	9	Raven and Breedlove 19921 (MICH), Raven, unpublished.
H. albiflorum	9	Stebbins, Jenkins, and Walters, 1953.
H. crepidispermum	9	Stebbins, Jenkins, and Walters, 1953.
H. crepidispermum	9	Powell and Turner, 1963.
H. gronovii	9	Jones, 1968.
H. irazuense	9	Beaman and Turner, 1962.

Methods

In the course of field work a search was made for any naturally occurring hybrids. Other priorities included the collection of live plants for breeding studies, the collection of seeds to grow into adult plants for breeding studies, establishment of pollinator-exclusion plots, and collection of pollen for pollen morphology studies.

In an effort to get field data on breeding systems, pollinator exclusion plots were established. Two locations were selected. At the first site, on Chipinque Mesa (near Monterrey, Nuevo León), ten flower stalks were wrapped with cheese cloth to exclude pollinators. The second site was at the base of Nevado de Toluca (near Toluca, State of Mexico), where 20 flower stalks were wrapped with cheese cloth. Any heads that were open, or that had completed flowering, were removed prior to wrapping. The stalks were then tied to a metal stake to prevent the stem from breaking when the cheese cloth became wet with the summer rains. The metal stakes had yellow plastic flags on which a request in Spanish was written "scientific investigation, please do not remove."

In 1986 a total of 37 plants was field collected. In order to bring the live material into the United States all soil was washed from the roots, the roots wrapped in moist tissue, and the plants placed in plastic bags with the appropriate collection numbers. These bags were placed in a larger plastic bag which was sealed and refrigerated during transit to Michigan State University where the plants were promptly potted individually into 4" round clay pots and placed in a greenhouse. The soil was a 9:1 mix of sterilized Bacto (a commercial mix of peat, ground bark, and perlite) and coarse sand.

Three plants died within a few days from apparent heat stress. The surviving plants were moved to a light bench indoors where they were exposed to a 12-hour light regime with an intensity of 180 microeinsteins. The plants began flowering within three weeks of potting.

Emasculation by anther excision was done as outlined by Guppy (1978) and Beaman (personal communication). All anthers in a head were excised at once, with one stroke of a razor blade. A new razor blade was used for each excision, and hands were washed between each excision. These precautions were taken to avoid contamination of the successive heads with pollen. Twenty heads in three species were utilized (Table 5).

Artificial self-pollination was attempted on flowers within the same head and on flowers in different heads on the same plant. Pollination of flowers within the same head was done by running a fine paint brush across the head to move pollen to all stigmas. The paint brush was swirled in 95% ethanol, washed with soap and water, rinsed for five minutes under running water and allowed to dry between uses. Pollination of two heads on the same plant was done by rubbing heads together. Two species and 18 heads were used for the self-pollination study (Table 6).

A control group to the above studies was established by selecting five plants which were not flowering at the same time as any other plants, and hence could not be used for hybridization work. No manipulation of flowers was done, including no wrapping to exclude pollinators (Table 7).

In an effort to determine best growing conditions for _Hieracium_ prior to further collections of the study species, 12 plants of _Hieracium fendleri_ A. Gray ssp. _fendleri_ were collected from the Santa

Rita Mountains of Pima County, Arizona in March 1987. Two were potted in their own soil and the rest were potted into a gradient of progressively more porous soil.

Two hundred forty-eight plants were field-collected in Mexico in 1987. They were immediately placed into 4" plastic pots in their own soil. As the plants generally grow in clumps this often meant that there were four to eight individuals per pot. The potted plants were kept in a portable greenhouse in the back of the field vehicle. This greenhouse was set outside whenever suitable conditions prevailed.

In order to bring the plants into the United States all soil had to be removed from the roots according to U. S. Department of Agriculture regulations. The majority of the soil was collected into paper bags for treatment by methyl bromide for 24 hours at the inspection station. The roots were washed to remove excess soil, wrapped in moist tissue, and the plants placed in plastic bags with appropriate collection numbers. These bags were sealed in larger plastic bags, wrapped in a towel to avoid ice damage to the outer leaves, and placed in an ice-filled cooler.

The plants remained in the cooler for five days prior to the return to Michigan State University where they were potted individually into 4" square plastic pots and placed on a growth bench indoors. Whenever possible the plants were re-potted into the soil from their collection site. When there was not enough native soil for all individual plants, a 9:1 mix of sterilized Bacto and coarse sand was used. If there were more than 10 individuals from a collection site, an additional soil mix was used. This was a 9:1:2 mixture of Bacto, coarse sand, and unsterilized soil from under the pines in the Beal Pinetum (Michigan

State University Campus). This last mix was used in an effort to determine if the plant death of the previous year was due to a lack of some mycorrhizal or other relationship with soil fungi found under pines.

On the growth bench the plants were exposed to a 13-hour day length and light intensity of 180 micro-einsteins. After four weeks, in an effort to induce flowering, the day length was increased to a 14-hour day, then, after an additional four weeks decreased to 12 hours. During this time the plants were stricken by successive infestations of disease and predatory insects. In sequential order the infestations and their treatments: thrips treated with Temik; powdery mildew with Benlate; white flies with Temik; fungus gnats (whose larvae eat soil fungus and damage plant roots) were treated with a Benlate soil drench; mealy bug treated with Malathion. Plants died at the rate of three to ten per week. None of the 248 field-collected plants flowered. Several plants sent up flower stalks, and had a few buds, but no buds opened, excluding the opportunity to utilize the plants collected in 1987 in breeding studies.

Seeds were field collected in 1986 and 1987. In some cases whole heads had been harvested. Where possible, counts were made of the total number of seeds (fruits) per head and the total number of viable seeds per head (Table 8). These seeds were subsequently included in the germination and growth studies outlined below.

Through trial and error a method for growing plants from seed was determined. It was found that surface sterilization of seeds was necessary due to the numerous fungi and bacteria present on the seed coat. The seeds were surface sterilized by the following process which started with a two-minute wash in 95% ethanol to remove waxes and enhance imbibition of water. They were then rinsed three times with distilled water, soaked for 8 hours in distilled water, then rinsed with a 10% bleach solution. This insured that any fungal spores that had germinated during the overnight soaking were killed. Three five-minute rinses with distilled water were required to remove all traces of the bleach solution. Seeds were then soaked in distilled water overnight and rinsed again. Once the seeds were sterilized, all equipment was surface sterilized and the remaining steps done in a laminar flow hood. Seeds were placed for germination in sterile petri plates with MSO nutrient agar solution as used in plant tissue culture. The plates were placed in a growth chamber under constant environmental conditions. Germinated seedlings were transferred into sterile MSO nutrient agar media in boxes known as GA-7's or Magenta-7's, commonly used in tissue culture. These were then kept in a growth chamber under constant environmental conditions.

After approximately two months in the GA-7's, the nutrient media became exhausted and the plants had to be transfered to fresh, sterile GA-7's with a nutrient agar solution. In the transfer process some root tips broke off. These tips were recovered for cytological work and processed according to the procedures outlined by Radford et al. (1974), but I was not able to find mitotically active cells.

The seeds collected in 1986 and grown in the GA-7's produced 74 individuals of a size suitable for flowering. However, all these plants were killed by a growth chamber malfunction prior to flowering.

A limited amount of tissue culture was attempted. The apical meristem and 4 to 10 leaf sections were isolated from five plants that appeared to be dying. These were sterilized, sectioned, placed in GA-

7's with MSO media that included growth hormones. The GA-7's were then placed in a growth chamber. The leaf tissue formed callus and three of the five meristem sections showed new growth. A growth chamber malfunction killed these tissues before significant results were obtained.

Results and discussion

Pollinator exclusion

All marker flags at both field localities were removed by local people during the period after they were installed and before my return to the sites. In most cases the cheese cloth had been removed from the plant and left on the ground, or was totally gone. Four of the ten stalks were found still wrapped at the Chipinque Mesa site and six of the 20 stalks were recovered from the Toluca site.

Total number of heads per stalk, total number of heads that were sufficiently mature for seed set to be determined, and the number of seeds set were recorded (Table 4). Heads were deemed mature enough for seed set to be determined if they had shed their corollas and had a conspicuous pappus. Generally it was easy to determine viable achenes because they were filled out, plump, and in most cases, of a darker color than those that were aborted.

Breeding Studies

Emasculation by anther excision was done on 20 heads of three species (Table 5). There was a total of 3 viable seeds recovered. This could indicate that the process of emasculation was so stressful to the plant that it failed to set much seed. Conversely, the three seeds may

Table 4. Results of pollinator exclusion study.

Site & taxon	# heads per stalk	# heads old enough to have seed (see text)	# seeds recovered
Toluca, Mexico H. mexicanum (Soule 1593)	8	1	0
	4	1	0
	4	1	0
	4	0	-
	4	1	0
	4	1	0
		Total	0
Chipinque, Nuevo Leon H. 'chipinque' (Soule 1696)	10	4	0
		.	3
		.	7
		.	0
	21	4	6
		.	0
		.	0
		larvae*	-
	23	0	-
	7	3	0
		.	0
		larvae*	-
		Total	16

*larvae indicates the larvae of Tephritid (Tephritidae) flies. The flies lay their eggs in Compositae heads and the larvae cause the formation of a protective gall as they eat the developing seed.

Table 5. Results of anther excision (emasculation) in selected species of Mexican *Hieracium*.

Species	Soule Collection Number	Number of heads	# of seeds recovered
H. crepidispermum	1398	3	0
		.	0
		.	0
			Total 0
H. abscissum	1407	6 +	1
			Total 1
H. mexicanum	1415	11	0
		.	1
		.	0
		.	0
		.	0
		.	1
		.	0
		.	0
		.	1
		.	0
		.	0
			Total 3

+ indicates that the heads opened in storage, exact counts per head not possible.

Table 6. Results of artificial self-pollination in selected species of Mexican *Hieracium*.

Species	Soule Collection Number	Crossed With	Number of replicates	# of seeds recovered
H. pringlei	1424T	other +	5	52
H. pringlei	1424W	other +	2	13
H. pringlei	1424T	same *	7	32
H. pringlei	1424T	same *	1	15
H. mexicanum	1393	same *	1	11

other + indicates that the heads were crossed with other heads on the same plant.

same * indicates that the flowers in the heads were crossed with other flowers in the same head (technique described in text).

Table 7. Control group for breeding system studies in Mexican *Hieracium*, heads left untouched and unwrapped.

Species	Soule Collection Number	Number of heads	# of seeds recovered
H. abscissum	1396	12 +	1
		4	0
		.	0
		.	0
		.	0
			Total 1
H. mexicanum	1392	7	0
		.	0
		.	0
		.	0
		.	0
		.	0
		.	0
			Total 0
H. mexicanum	1415	5	0
		.	0
		.	1
		.	0
		.	0
			Total 1
H. mexicanum	1419H	9	0
		.	0
		.	0
		.	1
		.	0
		.	0
		.	1
		.	0
		.	0
			Total 2
H. mexicanum	1419S	10	0
		.	0
		.	0
		.	0
		.	1
		.	2
		.	1
		.	0
		.	1
		.	0
			Total 5

+ indicates that the heads opened in storage, exact counts per head not possible.

Table 8. Counts of the number of seeds (fruits) per head in field-collected heads.

Species	Soule Collection Site Number	Soule Collection Number	# of seeds recovered
H. abscissum	4	1396	19
H. abscissum	4	1396	18
H. abscissum	4	1396	21
H. abscissum	4	1396	20
H. abscissum	4	1396	25
H. abscissum	4	1396	18
H. abscissum	4	1396	15
H. abscissum	10	1407	28
H. abscissum	10	1407	10
			Average 19.3
H. mexicanum	12	1414	15
H. mexicanum	13	1415	18
			Average 16.5
H. dysonymum	11	1411	12
H. dysonymum	11	1411	25
H. crepidispermum	8	1404	19
unidentified +	5B	none	15
unidentified +	5B	none	20
unidentified +	11	none	18

+ unidentified indicates that the heads were collected from a deceased plant. Positive identification not possible based on material available.

have been the result of incomplete anther excision and subsequent selfing, or they may have been due to pollination by white flies or fungus gnats because the heads were not wrapped to exclude pollinators after emasculation.

Artificial self-pollination was attempted on flowers within the same head and on flowers in different heads on the same plant using two species and 18 heads (Table 6). If these species are similar to pseudogamous apomicts which require pollen tube growth to begin before the female gametophyte forms the embryo, then the fruit set should have been higher, equivalent to the number set by plants in the field (Table 8).

A control group of five plants was established in which no manipulation of flowers was done, including no wrapping to exclude any pollinators (Table 7). The very low level of fruit set by these plants suggests that they are not apomictic. The few fruits set may have been caused by the actions of the fungus gnats or white flies which were present.

The sparsity of test replicates and lack of interspecific crosses were due to the constraints imposed by flowering periods. *Hieracium* flowers open for only a short time, and although pollen can be collected from flowers even after stigma receptivity has passed, the overlapping time frame necessary failed to occur. Another confounding factor was the fact that many buds aborted prior to opening, perhaps due to white fly feeding. This conclusion is backed by the findings of Snow and Stanton (1988) in which total fecundity of *Raphanus* was markedly reduced due to aphid feeding. Overall, the plants were stressed in "captivity" and died at the rate of one to three per week.

If one compares the results in Table 4 with those in Table 8, it can be seen that unwrapped heads have a higher number of seed set.

Wrapped heads of Hieracium 'chipinque' yielded 16 seeds from 12 heads, an average of 1.33 seeds per head, whereas H. abscissum unwrapped yielded an average of 19.3 seeds per head. Hieracium mexicanum had an average number of 16.5 seeds per head unwrapped and 0 seeds per head when wrapped. If the species are normally selfing, then these results indicate some perturbation to the system due to the wrapping. Otherwise, this demonstrates that outcrossing results in a greater number of seeds than does selfing.

When the results of the pollinator exclusion study (Table 4) are compared to the control group of the breeding studies (Table 7), an interesting similarity is seen. The control group, in which the heads were left alone and not wrapped, set virtually no seed as is the case in the pollinator exclusion studies. If one were to argue that the control group set no seed due to stressful environmental conditions, then it would follow that the artifically selfed group (Table 6) would also set no seed due to the same stressful environmental conditions. The artifically self-pollinated plants had virtually the same number of viable seed as the unwrapped plants in the native habitat (Table 8). This indicates that the control group set few seed because ovules were not fertilized and not because the plants were stressed.

Plants collected to test for optimal growth conditions

The Hieracium fendleri ssp. fendleri plants collected in Arizona in March of 1987 all died quickly, although individuals potted in their own soil survived almost three weeks longer than all others. This led to the conclusion that Hieracium species should be collected, brought back, and grown in their native soil whenever possible.

Conclusions

Overall, the data indicate that these Hieracium species are outcrossers that will, in some cases, set seed after selfing. This work does not find the plants apomictic. Further studies, under non-stressful conditions for the plants, should be done.

VESTITURE STUDY

Introduction

One important morphological character for species determination in *Hieracium* is the vestiture. Keys have been written based in considerable part on types and densities of hairs. Vestiture also has proven to be an aid to taxonomic classification in many other groups as seen in the work of Hardin (1957), Solbrig (1960, 1961), Anderson (1963), Webb and Carlquist (1964), Seith (1979), and Seith and Anderson (1982).

Almost since its inception, scanning electron microscopy (SEM) has been used for the examination of vestiture, in part because of the great depth of field, and in part due to the ease of preparation of samples (Hammond and Mahlberg 1973). Numerous workers have used SEM observations of vestiture as an aid to taxonomic classification, including Baum and Hadland (1973, 1975), Rollins and Banerjee (1975, 1979C), Anderson (1983), Hardin (1986), Hansen (1986), Healey, Mehta and Westerling (1986), Jones (1986), Wurdack (1986), Hardin and Bell (1986), Ehleringer and Cook (1987), Rosatti (1987), and Hannan (1988).

Preliminary work by Beaman with a dissecting microscope (unpublished) has identified five major types of vestiture in Mexican *Hieracium*:

1) tomentum at the base of the stems,

2) long pilose or hirsute vestiture on abaxial and adaxial surfaces of leaves,
3) lanate pubescence on leaves and stems,
4) glandular hairs on phyllaries,
5) presence or absence of pubescence on the stem at the base of the head.

This study investigated the vestiture at the base of stems, abaxial and adaxial surfaces of the leaves, phyllaries of mature heads, and stems at the base of heads.

Methods

Samples for the vestiture study were taken, with one exception, from the 1986 and 1987 collections of J. A. Soule et al. The exception was Hieracium pringlei, Rzedowski 30821 (MSC). All samples were from air dried herbarium specimens and were not treated or rehydrated for this study. Samples were selected from specimens based on three criteria. 1) Individuals of each taxon were selected from the extremes of the range, as well as from the center of the range; 2) plants that had been growing with other taxa of Hieracium were preferentially selected; 3) specimens were selected which included ample material so that the specimen would not be left depauperate from the modest amount of sample material removed.

Samples were taken from each of the following:

1) base of the stem (a 5 mm section immediately above the attachment of the uppermost leaf in the basal rosette);
2) abaxial surface of the youngest mature leaf of the basal rosette (a

10 mm long section starting at petiolar insertion into the blade);
3) adaxial surface of the youngest mature leaf of the basal rosette (a 10 mm long section immediately adjacent to the previous sample);
4) phyllary of a mature head at anthesis or prior to seed set;
5) a 5 mm section of stem at the base of a mature head.

These samples were mounted on large size JEOL stubs (24 mm diameter) using double stick tabs. Samples were prepared for viewing by grounding with carbon paint and coating with gold in an EM-Scope SC 500 sputter coater. The best coat thickness is 35 nanometers. Less of a coat, e.g. 21 nm, was not sufficient to eliminate charging.

A JEOL JSM-35CF scanning electron microscope located in the Center for Electron Optics at Michigan State University was used to view the samples. Settings were as follows: working distance 15, condenser lens 400, KV 15. Micrographs were taken using Polaroid Type 665 positive/negative film. A representative subset of all photographs taken is presented, by taxa, in Figures 6 through 12.

Based on the photographs of the samples, the kinds of hairs were defined following Payne (1978), and their presence or absence, and relative length evaluated where applicable. The vestiture information was quantified and these values, along with other key morphological characters, were entered into a data matrix for evaluation by the MVSP (MultiVariate Statistics Package) software developed by Kovach (1986). Presence of a character was valued at 0.99 and absence was valued at 0.01. This technique for handling categorical data intended for statistical analysis is used in the social sciences when the analysis includes categorical and numerical data. The compiled raw data are presented in Appendix II.

Due to the nature of the information gathered (a combination of quantitative and qualitative values) the appropriate statistical test was one that could take the two types of values into consideration and still yield meaningful results. There are two such tests available on the MVSP, Spearman's Rank Correlation and Average Linkage Cluster Analysis. Both tests were utilized. A series of correlations was run, first a combined correlation of all operational taxonomic units (OTUs) at once, then a series comparing each species to each other species. The Average Linkage Cluster Analysis was run on the same data groupings as the Spearman's Rank Correlations.

Results and Discussion

Figures 6 through 12 demonstrate the typical vestiture found in each species. Each figure contains six photographs. The first five photographs, A through E, represent the five samples taken from each specimen (see Methods). The sixth photograph in each figure is some interesting feature observed in detail.

The vestiture consists of four types: epicuticular waxes, glandular hairs, stellate hairs, and barbed hairs. Epicuticular waxes (see example Figure 9-F) are present in all samples of all individuals of Hieracium abscissum, H. pringlei, H. schultzii, and H. 'chipinque.' They are not found at all on any of the sampless of H. dysonymum, H. mexicanum, and H. 'potosi.' Thus these waxes can be used as a species-specific character.

On the phyllary glandular hairs and stellate hairs are present in all species. Barbed hairs are present only in Hieracium mexicanum and

H. schultzii. The phyllaries of all species show a rugose texture (see example Figure 7-F).

On the stem below the head glandular hairs are present in most samples. When present, the lengths of the glandular hairs were measured All samples of Hieracium dysonymum and H. 'potosi' lacked glandular hairs on the stem below the head. This factor, along with the absence of epicuticular waxes is a species-specific trait. Stellate hairs are present in all samples. Barbed hairs are present only on H. mexicanum and H. schultzii.

On the abaxial surface of the leaf glandular hairs are present in Hieracium dysonymum, H. mexicanum, and H. 'potosi.' Stellate hairs are present in only two samples from two different species. Barbed hairs are present in all species. When possible, length of the barbed hairs was measured. The relative lengths of the barbs on the hairs were evaluated as "long" or "short," long referring to those barbs mostly longer than 40 micrometers, and short those between 10 and 35 micrometers. An example of a short barbs is found in Figure 6-E. This can be compared to the long barbs which are found only in Hieracium pringlei, Figure 9-E. This factor is a species-specific trait. The presence or absence of glandular hairs on leaves was thought to be species-specific. They were not found on the standard samples of Hieracium abscissum; however, they were found on the sample of a very young H. abscissum leaf (Figure 6-F). The fact that the glands were not found on mature leaves of the species may indicate that they are lost as the leaf matures, or that this is an aberrant sample, or that they were broken off during field collection of the plant.

On the adaxial surface of the leaf glandular hairs are present on some samples. Stellate hairs are mostly lacking on lower leaf surfaces.

Figure 6. Scanning electron micrographs of the vestiture of *Hieracium abscissum*.

A). Phyllary with waxes, glandular and stellate hairs.

B). Stem below the head with waxes, glandular and stellate hairs.

C). Upper surface of the leaf with waxes and short-barbed hairs.

D). Lower surface of the leaf with waxes and short-barbed hairs.

E). Base of the stem with short-barbed hairs; waxes lacking.

F). Upper surface of an immature leaf, note glandular hairs.

The bar on all photos indicates 100 micrometers.

Photos of samples taken from the following specimens:

A. *Soule 1408*
B. *Soule 1573*
C. *Soule 1408*
D. *Soule 1648*
E. *Soule 1408*
F. *Soule 1408*

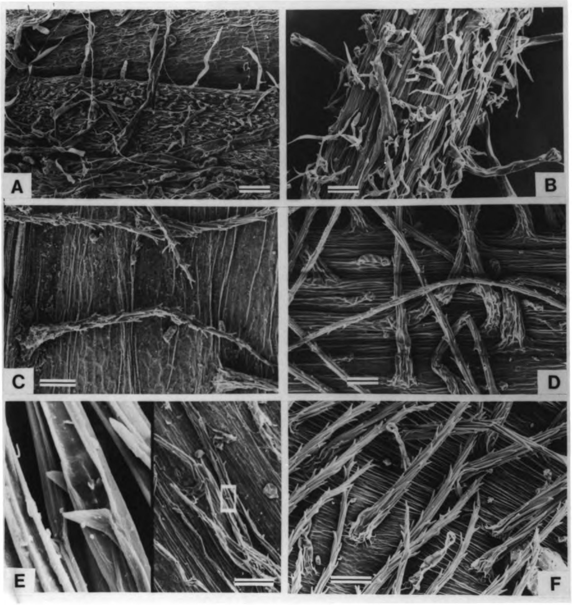

Figure 6

Figure 7. Scanning electron micrographs of the vestiture of Hieracium dysonymum.

A). Phyllary with glandular and stellate hairs; waxes lacking.

B). Stem below the head with stellate hairs; waxes lacking.

C). Upper surface of the leaf with glandular and short-barbed hairs; waxes lacking.

D). Lower surface of the leaf with glandular and short-barbed hairs; waxes lacking.

E). Base of the stem with glandular and short-barbed hairs; waxes lacking.

F). Phyllary surface, note rugose texture and lack of waxes.

The bar on all photos indicates 100 micrometers.

Photos of samples taken form the following specimens:

A. Soule 1421 B. Soule 1421
C. Soule 1412 D. Soule 1421
E. Soule 1421 F. Soule 1412

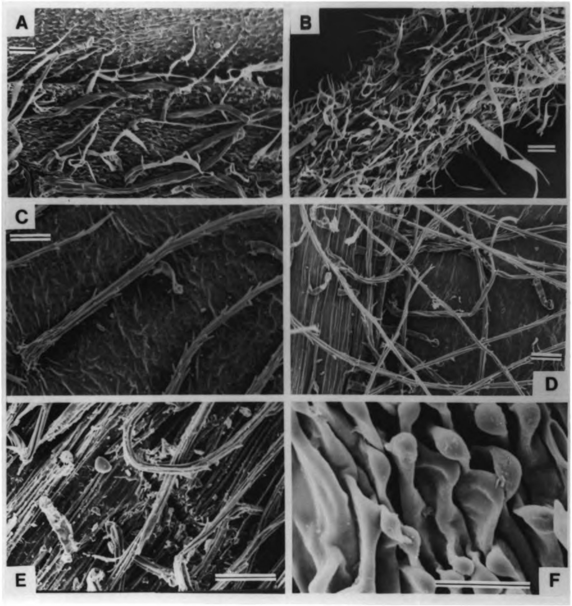

Figure 7

Figure 8. Scanning electron micrographs of the vestiture of *Hieracium mexicanum*.

A). Phyllary with glandular, stellate and short-barbed hairs; waxes lacking.

B). Stem below the head with glandular, stellate and short-barbed hairs; waxes lacking.

C). Upper surface of the leaf with glandular, stellate and short-barbed hairs; waxes lacking.

D). Lower surface of the leaf with glandular, stellate and short-barbed hairs; waxes lacking.

E). Base of the stem with glandular, stellate and short-barbed hairs; waxes lacking.

F). Phyllary of specimen from Iztaccíhuatl, above timberline. Note density of short-barbed hairs.

The bar on all photos indicates 100 micrometers.

Photos of samples taken from the following specimens:

A. *Soule 1420* B. *Soule 1420*
C. *Soule 1420* D. *Soule 1420*
E. *Soule 1420* F. *Soule 1614*

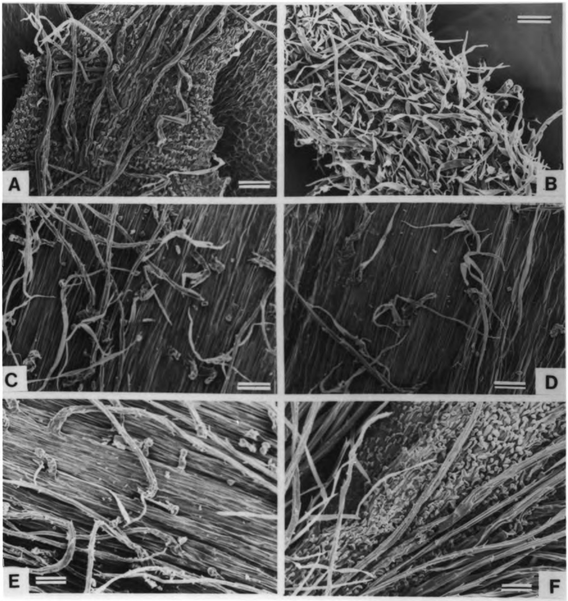

Figure 8

Figure 9. Scanning electron micrographs of the vestiture of *Hieracium pringlei*.

A). Phyllary with waxes, glandular and stellate hairs.

B). Stem below the head with waxes, glandular and stellate hairs.

C). Upper surface of the leaf with waxes, and long-barbed hairs.

D). Lower surface of the leaf with waxes, and long-barbed hairs.

E). Base of the stem long-barbed hairs; waxes lacking.

F). Stem below the head, note waxes and the base of a stellate hair.

Bar equals 1 micrometer.

The bar on all photos indicates 100 micrometers unless noted otherwise.

Photos of samples taken from the following specimens:

A. *Soule 1579*	B. *Soule 1664*
C. *Soule 1664*	D. *Soule 1579*
E. *Soule 1664*	F. *Soule 1664*

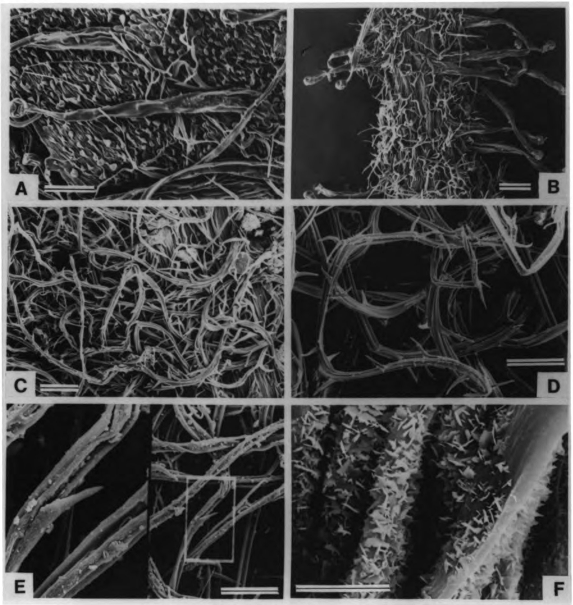

Figure 9

Figure 10. Scanning electron micrographs of the vestiture of _Hieracium schultzii_.

A). Phyllary with waxes, stellate, glandular, and short-barbed hairs.

B). Stem below the head with waxes, stellate, glandular and short-barbed hairs.

C). Upper surface of the leaf with waxes and short-barbed hairs.

D). Lower surface of the leaf with waxes and short-barbed hairs.

E). Base of the stem with waxes and short-barbed hairs.

F). Phyllary, note rugose texture, waxes and portion of a stellate hair. Bar equals 10 micrometers.

The bar on all photos indicates 100 micrometers unless otherwise noted.

Photos of samples taken from the following specimens:

A. _Soule 1409_ B. _Soule 1572_
C. _Soule 1549_ D. _Soule 1549_
E. _Soule 1409_ F. _Soule 1549_

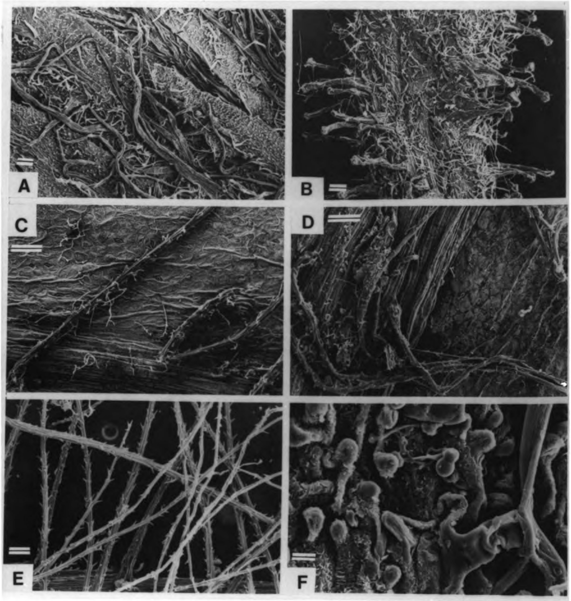

Figure 10

Figure 11. Scanning electron micrographs of the vestiture of _Hieracium 'chipinque_.'

A). Phyllary with waxes, glandular and stellate hairs.

B). Stem below the head with waxes, glandular and stellate hairs.

C). Upper surface of the leaf with waxes, and short-barbed hairs.

D). Lower surface of the leaf with waxes, and short-barbed hairs.

E). Base of the stem with waxes, and short-barbed hairs.

F). Detail of the stem below the head, note waxes on wrinkled epidermis, stellate hairs and stomate. Bar equals 10 micrometers.

The bar on all photos indicates 100 micrometers unless otherwise noted.

Photos of samples taken from the following specimens:

A. _Soule 1485_ B. _Soule 1485_
C. _Soule 1485_ D. _Soule 1485_
E. _Soule 1485_ F. _Soule 1485_

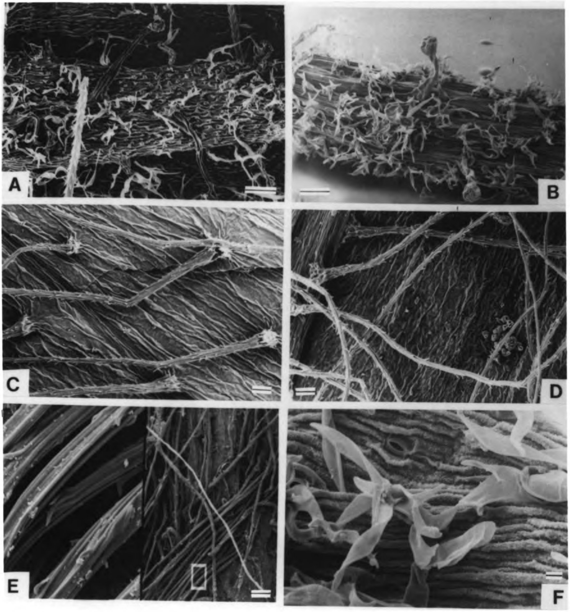

Figure 11

Figure 12. Scanning electron micrographs of the vestiture of _Hieracium 'potosi._'

A). Phyllary with glandular and stellate hairs; waxes lacking.

B). Stem below the head with stellate hairs; waxes lacking.

C). Upper surface of the leaf with glandular and short-barbed hairs; waxes lacking.

D). Lower surface of the leaf with glandular and short-barbed hairs; waxes lacking.

E). Base of the stem with glandular and short-barbed hairs; waxes lacking.

F). Cross section of stigma, broken at time of collection. Bar equals 10 micrometers.

The bar on all photos indicates 100 micrometers unless otherwise noted.

Photos of samples taken from the following specimens:

A. _Soule 1507_ B. _Soule 1507_
C. _Soule 1507_ D. _Soule 1507_
E. _Soule 1507_ F. _Soule 1507_

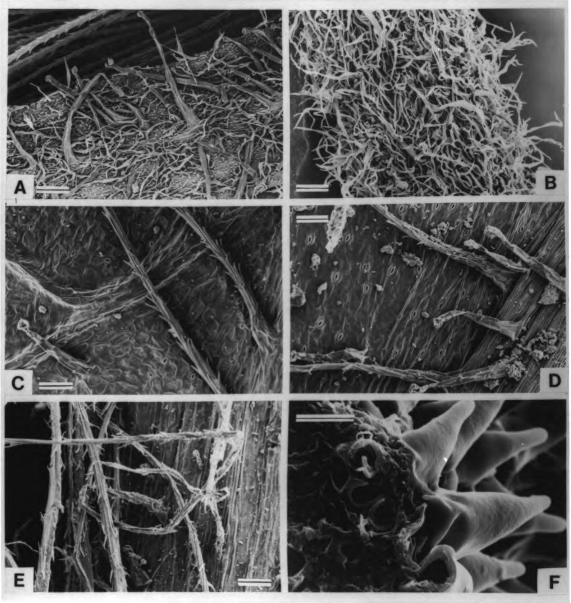

Figure 12

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Barbed hairs are found in all species. The relative lengths of the barbs on the hairs were also evaluated. Pubesence on the lower surface of the leaf was commonly found on the mid-rib, as seen in Figures 7-D, 10-D, 11-D, and 12-D. This may serve as a deterrent to insect herbivory (Becerra and Ezcurra 1986).

On the stem at the base of the plant, glandular hairs are found only in Hieracium dysonymum, H. mexicanum, and H. 'potosi.' Stellate hairs are found on all samples of H. mexicanum and on no other samples and can thus be considered a species-specific trait. Barbed hairs are present on all species. The relative lengths of the barbs on the barbed hairs were also evaluated. The presence or absence of epicuticular waxes on these samples was frequently hard to determine as the stems had often been handled extensively during collection.

The vestiture of an individual plant can vary over the course of a season, depending on environmental conditions the individual is subjected to, as shown by the work of Ehleringer and Cook (1987), Ehleringer and Werk (1986) and Becerra and Ezcurra (1986). Therefore, the vestiture data were recorded as length and presence or absence of a particular type of hair, and the factor of density was not used in the analysis.

The results of the vestiture study were evaluated by Spearman's Rank Correlation using Kovach's (1986) MVSP program. The correlations are presented in Tables 9-12.

Spearman's Rank Correlation gives an estimate of the similarity between specimens, based on the values of the data input. This similarity can be a positive or negative value. The closer the value is to +1, the higher the correlation. For example, in Table 9, the value

1.00 appears when a specimen is compared to itself. The value 1.00 also appears in two other places in Table 9 where two specimens are identical as to characters surveyed.

One clear-cut example of the test results is seen with the *Hieracium mexicanum* correlations; *H. mexicanum* correlates generally negatively with other species, although somewhat positively with *H. dysonymum*, and *H.* '*potosi*.'

Table 9 yields a good indication of overall infrageneric grouping in the species studied. If one adds the categories of 'headedness,' i.e. many heads per stalk versus few heads per stalk, and the pollen character of straight versus curved spines (discussed in section on pollen) there is a fairly clear-cut split. The many headed, curved-spine pollen species are *Hieracium abscissum*, *H. schultzii*, and *H.* '*chipinque*.' These species are highly correlated with one another, and lowly or negatively correlated with the remaining species. The remaining group would be the few headed, straight-spined group which includes *Hieracium dysonymum*, *H. mexicanum*, *H. pringlei*, and *H.* '*potosi*.'

Spearman's Rank Correlation was next done on the infrageneric groups of many-headed or few-headed taxa. The comparison of *H. abscissum*, *H. schultzii*, and *H.* '*chipinque*' (Table 10) indicates that *H.* '*chipinque*' is more closely allied to *H. abscissum* than it is to *H. schultzii*. Note that in two places in Table 10, although all specimens are from different populations, the value of 1.00 appears for different collections of the same species. This indicates that the different populations yield individuals that are virtually identical based on the data surveyed. It would thus appear that plants with less highly correlated values can indeed be thought of as separate species and not

Table 9. Spearman's Rank Correlation Coefficients for the vestiture data of all OTUs in the study.

	abs1408	abs1573	abs1648	dys1412	dys1421	dys1550	mex1420	mex1593	mex1614	pri1575	pri1664	pr30821	nul1519	nul1523	sch1409	sch1549	sch1572	chi1485	pot1507
abs1408	1																		
abs1573	0.88	1																	
abs1648	0.88	1	1																
dys1412	0.23	0.46	0.46	1															
dys1421	0.16	0.39	0.39	0.94	1														
dys1550	0.67	0.81	0.81	0.63	0.57	1													
mex1420	-0.32	-0.12	-0.12	0.45	0.51	0.09	1												
mex1593	-0.15	0.04	0.04	0.44	0.37	0.23	0.76	1											
mex1614	-0.10	0.08	0.08	0.31	0.26	0.24	0.66	0.90	1										
pri1575	0.58	0.74	0.74	0.37	0.30	0.71	-0.26	-0.09	-0.03	1									
pri1664	0.55	0.72	0.72	0.40	0.32	0.73	-0.24	-0.06	-0.06	0.94	1								
pr30821	0.46	0.63	0.63	0.30	0.22	0.62	-0.34	-0.03	0.11	0.86	0.81	1							
nul1519	0.40	0.57	0.57	0.41	0.35	0.49	-0.13	0.12	0.21	0.59	0.60	0.74	1						
nul1523	0.40	0.57	0.57	0.41	0.35	0.49	-0.13	0.12	0.21	0.59	0.60	0.74	1	1					
sch1409	0.75	0.87	0.87	0.39	0.31	0.72	-0.09	0.18	0.28	0.60	0.57	0.66	0.64	0.64	1				
sch1549	0.74	0.87	0.87	0.39	0.32	0.72	-0.09	0.18	0.28	0.60	0.57	0.66	0.64	0.64	1.00	1			
sch1572	0.81	0.93	0.93	0.44	0.37	0.77	-0.03	0.15	0.19	0.67	0.65	0.56	0.53	0.53	0.94	0.94	1		
chi1485	0.81	0.92	0.92	0.52	0.46	0.87	-0.02	0.13	0.16	0.80	0.79	0.70	0.63	0.63	0.84	0.84	0.89	1	
pot1507	0.02	0.10	0.10	0.70	0.63	0.29	0.58	0.58	0.44	-0.01	0.02	-0.08	0.06	0.06	0.07	0.07	0.11	0.22	1

Table 10. Spearman's Rank Correlation Coefficients for the vestiture data of *Hieracium abscissum*, *H. schultzii*, and *H.* '*chipinque*.'

	abs1408	abs1573	abs1648	sch1409	sch1549	sch1572	chi1485
abs1408	1						
abs1573	0.88	1					
abs1648	0.88	1	1				
sch1409	0.75	0.87	0.87	1			
sch1549	0.74	0.87	0.87	1.00	1		
sch1572	0.81	0.93	0.93	0.94	0.94	1	
chi1485	0.81	0.92	0.92	0.84	0.84	0.89	1

Table 11. Spearman's Rank Correlation Coefficients for the vestiture data of *Hieracium dysonymum*, *H. pringlei*, and *H.* '*potosi*.'

	dys1412	dys1421	dys1550	pri1575	pri1664	pr30821	nul1519	nul1523	pot1507
dys1412	1								
dys1421	0.94	1							
dys1550	0.63	0.57	1						
pri1575	0.37	0.30	0.71	1					
pri1664	0.40	0.32	0.73	0.94	1				
pr30821	0.30	0.22	0.62	0.86	0.81	1			
nul1519	0.41	0.35	0.49	0.59	0.60	0.74	1		
nul1523	0.41	0.35	0.49	0.59	0.60	0.74	1	1	
pot1507	0.70	0.63	0.29	-0.01	0.02	-0.08	0.06	0.06	1

Table 12. Spearman's Rank Correlation Coefficients for the vestiture data of *Hieracium dysonymum*, *H. mexicanum*, and *H.* '*potosi*.'

	dys1412	dys1421	dys1550	mex1420	mex1593	mex1614	pot1507
dys1412	1						
dys1421	0.94	1					
dys1550	0.63	0.57	1				
mex1420	0.45	0.51	0.09	1			
mex1593	0.44	0.37	0.23	0.76	1		
mex1614	0.31	0.26	0.24	0.66	0.90	1	
pot1507	0.70	0.63	0.29	0.58	0.58	0.44	1

Table 13. Average Linkage Cluster Analysis of vestiture data of all taxa of *Hieracium* in the study.

NODE	GROUP 1	GROUP 2	AVERAGE SIMILARITY	NUMBER OF OBJECTS IN FUSED GROUP
1	abs1573	abs1648	1.00	2
2	nul1519	nul1523	1.00	2
3	sch1409	sch1549	1.00	2
4	dys1412	dys1421	0.94	2
5	pri1575	pri1664	0.94	2
6	NODE 3	sch1572	0.94	3
7	NODE 1	chi1485	0.92	3
8	mex1593	mex1614	0.90	2
9	NODE 7	NODE 6	0.88	6
10	NODE 5	pr30821	0.83	3
11	abs1408	NODE 9	0.81	7
12	NODE 11	dys1550	0.77	8
13	mex1420	NODE 8	0.71	3
14	NODE 4	pot1507	0.66	3
15	NODE 12	NODE 10	0.65	11
16	NODE 15	NODE 2	0.58	13
17	NODE 14	NODE 13	0.44	6
18	NODE 16	NODE 17	0.15	19

Figure 13. Dendrogram based on the Cluster Analysis of all OTUs of Mexican *Hieracium* in this study.

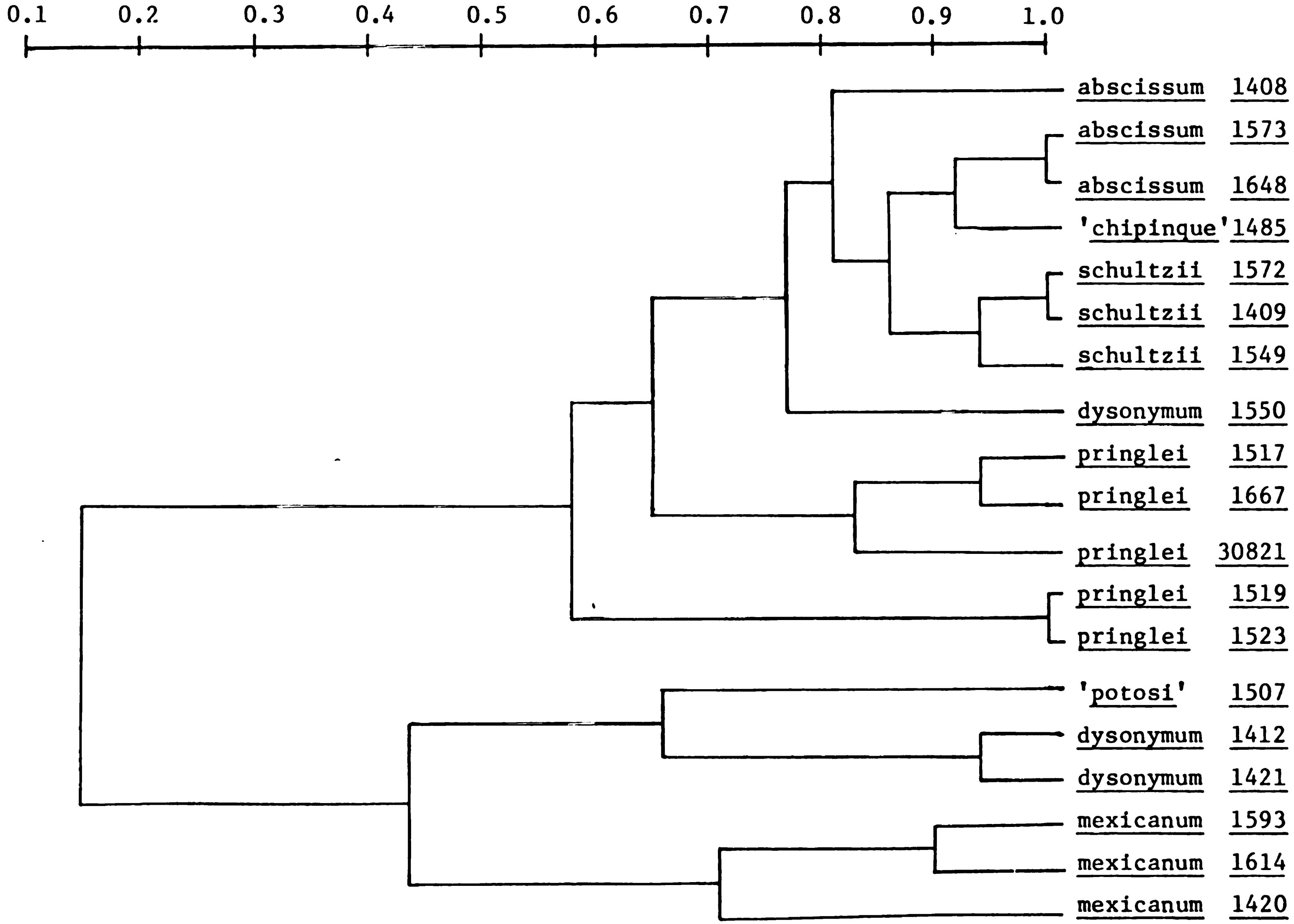


Table 14. Average Linkage Cluster Analysis of vestiture data for *Hieracium abscissum*, *H. schultzii*, and *H. 'chipinque.'*

NODE	GROUP 1	GROUP 2	AVERAGE SIMILARITY	NUMBER OF OBJECTS IN FUSED GROUP
1	abs1573	abs1648	1.00	2
2	sch1409	sch1549	1.00	2
3	NODE 2	sch1572	0.94	3
4	NODE 1	chi1485	0.92	3
5	NODE 4	NODE 3	0.88	6
6	abs1408	NODE 5	0.81	7

Figure 14. Dendrogram based on the Cluster Analysis of *Hieracium abscissum*, *H. schultzii*, and *H. 'chipinque'*.

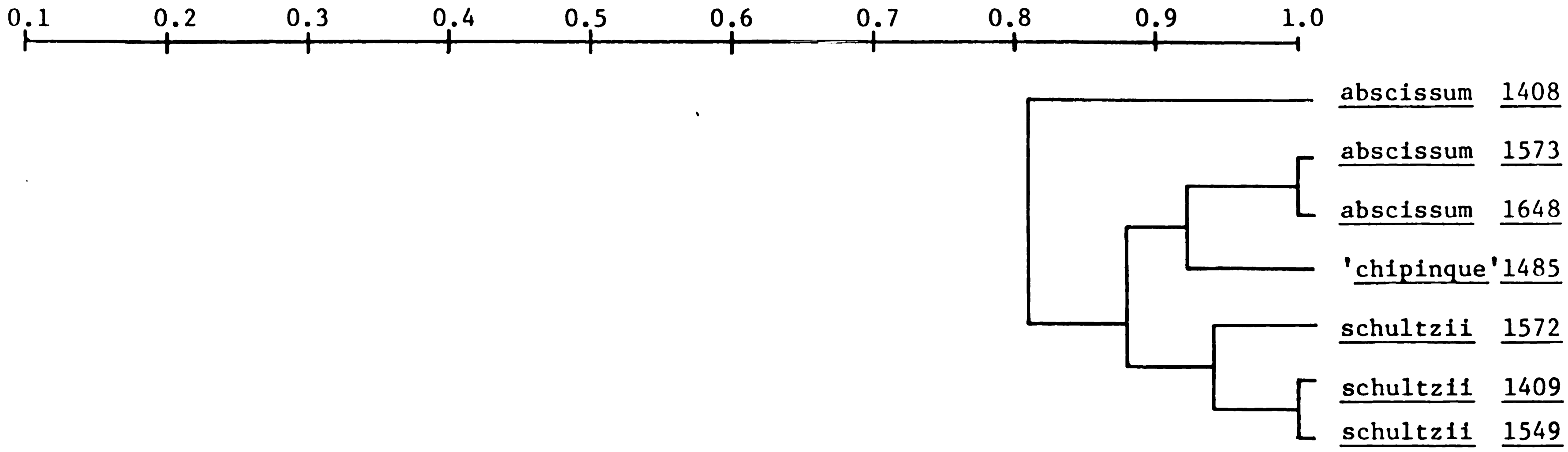


Table 15. Average Linkage Cluster Analysis of vestiture data for *Hieracium dysonymum*, *H. pringlei*, and *H. 'potosi.'*

NODE	GROUP 1	GROUP 2	AVERAGE SIMILARITY	NUMBER OF OBJECTS IN FUSED GROUP
1	nu11519	nu11523	1.00	2
2	dys1412	dys1421	0.94	2
3	pri1575	pri1664	0.94	2
4	NODE 3	pr30821	0.83	3
5	dys1550	NODE 4	0.69	4
6	NODE 2	pot1507	0.66	3
7	NODE 5	NODE 1	0.60	6
8	NODE 6	NODE 7	0.28	9

Figure 15. Dendrogram based on the Cluster Analysis of *Hieracium dysonumum*, *H. pringlei*, and *H. 'potosi.'*

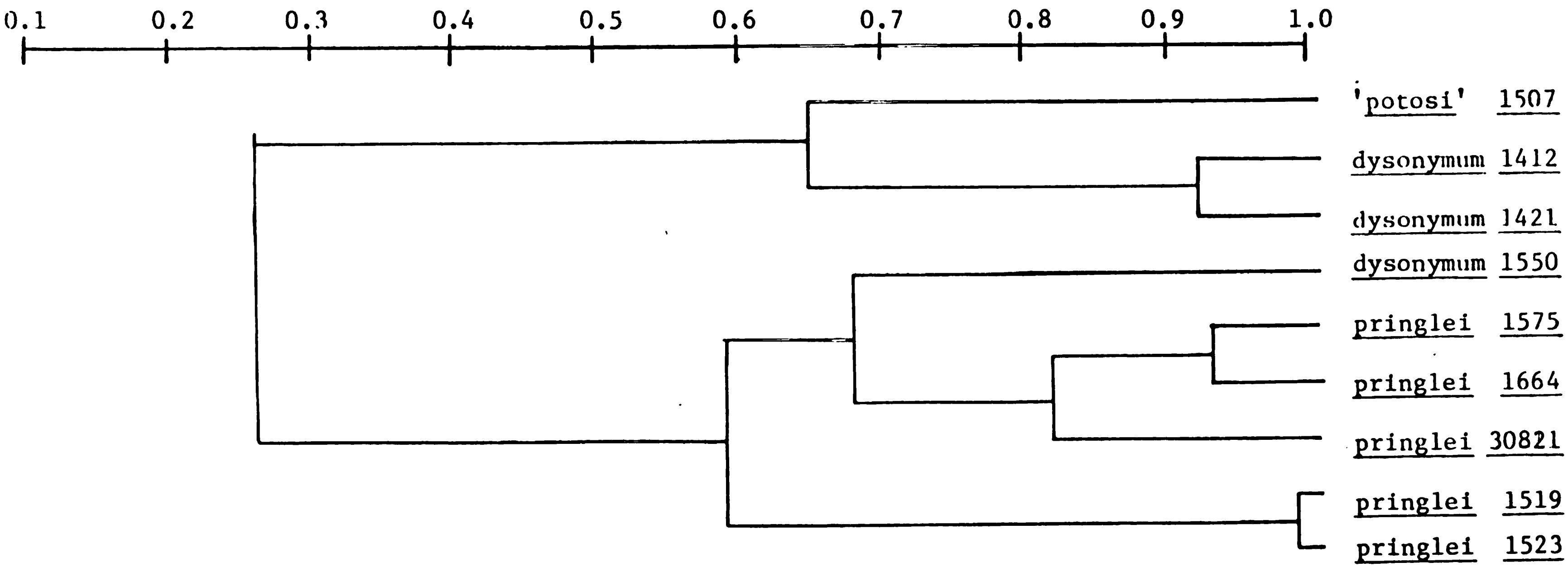
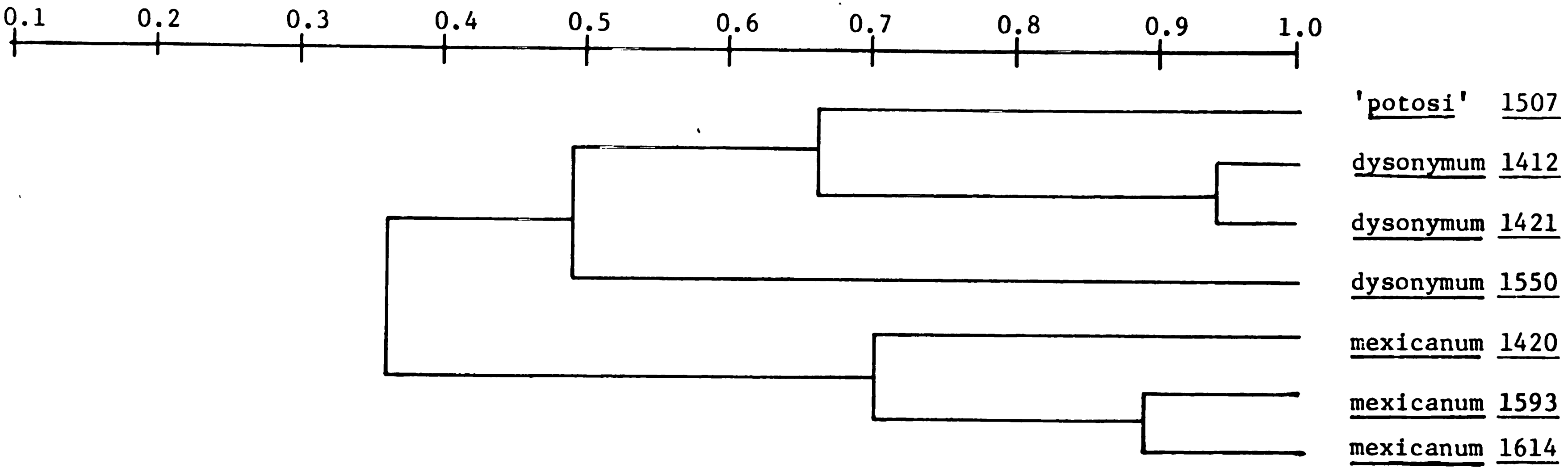


Table 16. Average Linkage Cluster Analysis of vestiture data for *Hieracium dysonymum*, *H. mexicanum*, and *H. 'potosi.'*

NODE	GROUP 1	GROUP 2	AVERAGE SIMILARITY	NUMBER OF OBJECTS IN FUSED GROUP
1	dys1412	dys1421	0.94	2
2	mex1593	mex1614	0.90	2
3	mex1420	NODE 2	0.71	3
4	NODE 1	pot1507	0.66	3
5	NODE 4	dys1550	0.50	4
6	NODE 5	NODE 3	0.37	7

Figure 16. Dendrogram based on the Cluster Analysis of *Hieracium dysonymum*, *H. mexicanum*, and *H. 'potosi.'*



just different populations.

The correlations between Hieracium dysonymum, H. pringlei, and H. 'potosi' (Table 11) show that H. 'potosi' is, in part, negatively correlated to H. pringlei; H. pringlei is also fairly lowly correlated to H. dysonymum. Combined, this indicates that H. 'potosi' is not very likely to be a hybrid of H. dysonymum with H. pringlei.

Hieracium 'potosi' is more closely correlated to H. mexicanum than it is to H. pringlei (Table 12). H. 'potosi' is more highly correlated to H. dysonymum than it is to H. mexicanum, except for the H. dysonymum population that is closest to it in range (Soule 1550). This individual also does not correlate highly with the other two samples of its species. If one averages the correlations of H. 'potosi' with H. dysonymum, and H. 'potosi' with H. mexicanum, they average to 54.0 and 53.3 respectively. However, based on the fact that H. dysonymum (Soule 1550) is so slightly correlated with other specimens of its species, and eliminating that value from the averaging, one gets an average correlation of H. 'potosi' with H. dysonymum, and H. 'potosi' with H. mexicanum of 66.5 and 53.3 respectively. This suggests that H. 'potosi' is more closely allied to H. dysonymum than to H. mexicanum.

The results of the Spearman's Rank Correlation were next evaluated by Average Linkage Cluster Analysis using Kovach's (1986) MVSP program. The Cluster Analysis results are presented in Tables 13 through 16. This information was then utilized to formulate the dendrograms presented in Figures 13 through 16. The lengths of the branches in the dendrograms are taken from the reported average similarity values.

Table 13 and Figure 13 show the results of Cluster Analysis of all taxa in this study combined. Note that Hieracium 'chipinque' is more similar to *H. abscissum* than *H.* '*potosi*' is to *H. dysonymum*. Based on the samples selected, *H. pringlei*, *H. mexicanum*, and *H. dysonymum* all show a higher degree of polytypy than do *H. schultzi* or *H. abscissum*; indeed, *H.* '*chipinque*' is more similar to *H. abscissum* than the *H. mexicanum* samples are to one another.

Table 14 and Figure 14 show the results of Cluster Analysis of *Hieracium abscissum*, *H. schultzii* and *H.* '*chipinque*.' This is the same as the information presented in Table 13 and Figure 13, yet it is easier to note the fact that *H.* '*chipinque*' is more closely linked to two of the *H. abscissum* collections (*Soule 1573*, *1648*) than they are to another *H. abscissum* sample (*Soule 1408*).

Table 15 and Figure 15 show the results of Cluster Analysis of *Hieracium dysonymum*, *H. pringlei*, and *H.* '*potosi*.' The length of the connecting branches becomes longer but overall the clusters are equivalent to those in Table 13 and Figure 13.

Table 16 and Figure 16 show the results of Cluster Analysis of *Hieracium dysonymum*, *H. mexicanum*, and *H.* '*potosi*.' By comparing Figure 15 to Figure 16 it is once again indicated that *Hieracium dysonymum* and *H.* '*potosi*' are more closely linked to one another than they are to *H. mexicanum* or *H. pringlei*. The comparison of the two dendrograms also indicates that *H. mexicanum* is more closely related to *H. dysonymum*/'*potosi*' than is *H. pringlei*.

Conclusions

Evaluation of vestiture data using Spearman's Rank Correlation and Average Linkage Cluster Analysis indicates that there are two major groupings of the *Hieracium* species studied here. One group is the

Hieracium abscissum-*H. schultzii* group to which *H.* '*chipinque*' belongs; *H.* '*chipinque*' is also shown to be closely related to *H. abscissum*, indeed, in scanning electron micrographs they are impossible to tell apart. The other group is the *Hieracium dysonymum*-*mexicanum* group to which *H.* '*potosi*' belongs. *Hieracium* '*potosi*' is shown to be more closely allied to *H. dysonymum* than to *H. mexicanum*, but not as closely linked as *H.* '*chipinque*' is to *H. abscissum*. Based on this evidence *H.* '*chipinque*' should either be submerged into *H. abscissum*, or should be given a low, perhaps varietal level ranking. *Hieracium* '*potosi*' is distinct enough from *H. dysonymum* to be given a higher level ranking, variety if *H.* '*chipinque*' is submerged, and subspecies if it is not.

Hieracium schultzii is determined to be segregated from, though closely related *H. abscissum*. *Hieracium pringlei* is a highly polytypic taxon yet it maintains a clear-cut species identity.

POLLEN STUDIES

Introduction

Pollen grains have been utilized as an aid to clarifying the systematics of numerous groups. Wodehouse did a series of investigations into Compositae pollen using light microscopy, beginning in 1926 and running through 1945, and could be viewed as one of the founding fathers of this line of research. He found it possible to trace phylogenetic trends in the Compositae based on palynological evidence.

In early palynological work, artists' renditions were used to record investigations (i.e. Wodehouse 1930). Later, photographs were used but, due to the very narrow depth of field in light microscopy, most images appeared at least partially blurry. Often artists' renditions were used to try to clarify the photographs, as seen in the work of Carlquist (1961) and Canright (1953). Workers often used overall pollen size to make species distinctions since fine surface detail is difficult to view or evaluate with light microscopy (Stone 1963; Kapadia and Gould 1964; Buchholz and Kaeiser 1940).

The advent of scanning electron microscopy (SEM) revolutionized pollen viewing by providing a greater depth-of-field than light microscopy, resulting in a very sharp, virtually three-dimensional photographic image, and eliminating the vagrancies of recording by a non-artist's hand (Martin 1969). Furthermore, the resolution in SEM is such that surface features not visible with light microscopy can be resolved and accurately measured. The relative ease of preparation is an added attraction to its use (Martin and Drew 1969, 1970; Hanks and Fairbrothers 1970).

The SEM has been used to survey the pollen grains of many groups and has proved a valuable aid in systematic studies (Skvarla and Turner 1966; Lewis 1977). Workers have found that measurements of various external features such as length of spines, lacunae and annulus features, and texture and patterning of the exine of the pollen grains can often clearly differentiate species. A partial list of taxonomic work based in part on SEM of pollen includes the work of M. Takahashi (1987), H. Takahashi (1986), Elisens (1986), Terrell et al. (1986), Donoghue (1985), vanWyk and Dedekind (1985), Constance and Chuang (1982), Rollins and Banerjee (1979A and 1979B), Keeley and Jones (1977), Anderson and Gensel (1976), Baum et al. (1970, 1971), Jones (1970). Of particular note is the work by Baum, Bassett and Crompton (1971) which combined light microscopy with SEM, and resulted in a key to 52 species of _Tamarix_ based on pollen morphology. Of greater significance to the work here is Jones' 1970 study of _Vernonia_ (Compositae). Jones combined scanning electron micrographs with hybridization experiments and cytological evidence to clarify relationships in the genus.

SEM examination of pollen was conducted to determine species affiliation in the _Hieracium_ taxa involved in this study. Pollen was field-collected from all taxa except _H. schultzii_ which was collected from unopened anthers of a dried specimen.

Methods

Pollen was field-collected for SEM observation by carrying the SEM stubs into the field and applying double-stick tabs to the stubs immediately prior to pressing them into the open florets of Hieracium heads. Pollen was obtained at 24 collection sites. Voucher specimens were collected once the pollen sample was taken. All collections are those of J. A. Soule and J. P. Bodeau in 1987. Voucher specimens are in the Beal-Darlington Herbarium, Michigan State University (MSC).

Pollen stubs were prepared for viewing by sputter-coating with gold in an EM-Scope SC 500 sputter coater. Three coating thicknesses were tried, 21 nm, 14 nm, and 10.5 nm. The 14 nm coat resulted in the best compromise between absolute veiwing clarity and lack of charging.

A JEOL JSM-35CF scanning electron microscope at the Center for Electron Optics at Michigan State University was used to view the pollen. Settings were as follows: working distance 15; condenser lens 400; KV 15. Micrographs were taken using Polaroid Type 665 positive/negative film. Figures 17 and 18 contain a representative sample of the photographs obtained.

A series of measurements was taken: overall grain diameter, spine height, spine height above the pits, and number of spines on the annulus and lacunae. The diameter was calculated by placing a piece of tracing paper over the photograph and tracing the outermost edges of the pollen, including spines. The diameters were then calculated from the circle created. Total length of the spines located on the annulus (around the germinal pore) was measured. A flexible ruler was used so that in the case of curved spines the entire length could be evaluated. An additional measurement of the length of spines above the pits was taken and the percentage of spine above the pits determined. The pits characteristically occur on only the lower half of the spine. In cases where the spines on the annulus were not visible, spines surrounding the lacunae were used. Results of these measurements are in Table 17.

A pollen character that seemed to vary between taxa was the number of spines on the annulus and around the lacuna. The values vary between 8 and 12, and are always even numbers. Counts were taken in as many instances as were possible.

It should be mentioned that all pollen work was done "blind," that is without identifying the species from which the pollen was collected until final tabulation of results.

Results and Discussion

Based on external pollen morphology, it is easy to separate the Mexican species of Hieracium investigated into two groups, the "curved-spine" group and the "straight-spine" group as seen in Figure 17; on the left are the straight-spine group, Hieracium dysonymum, H. mexicanum, and H. 'potosi' and on the right are the curved-spine group, H. abscissum, H. schultzii, and H. 'chipinque.' The two groups actually correspond well with the plants' growth form. The many headed species -- H. abscissum, H. schultzii, and H. 'chipinque,' have curved spines; the few headed species -- H. dysonymum, H. mexicanum, and H. 'potosi,' have straight spines.

Hieracium pollen is spherical, triporate, echinate with scrobiculate (pitted) spines, and has a lacuna immediately adjacent to

Figure 17. Field-collected *Hieracium* pollen.

A). *H. dysonymum* B). *H. abscissum*

C). *H. mexicanum* D). *H. schultzii*

E). *H.* '*potosi*' F). *H.* '*chipinque*'

The bar on all photos indicates 10 micrometers.

Voucher specimens for samples:

A. *Soule 1586* B. *Soule 1573*
C. *Soule 1593* D. *Soule 1409*
E. *Soule 1507* F. *Soule 1485*

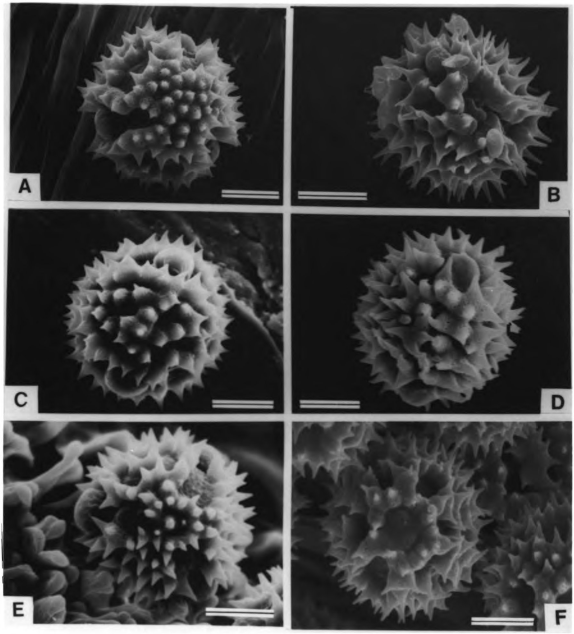


Figure 17

Figure 18. Field-collected *Hieracium* pollen which has germinated.

A). *H. abscissum*
B). *H. dysonymum*
C). *H. mexicanum*
D). *H. pringlei*
E). *H.* '*chipinque*'
F). *H.* '*potosi*'

The bar on all photos indicates 10 micrometers.

Voucher specimens for samples:

A. *Soule 1654*
B. *Soule 1586*
C. *Soule 1612*
D. *Soule 1516*
E. *Soule 1485*
F. *Soule 1507*

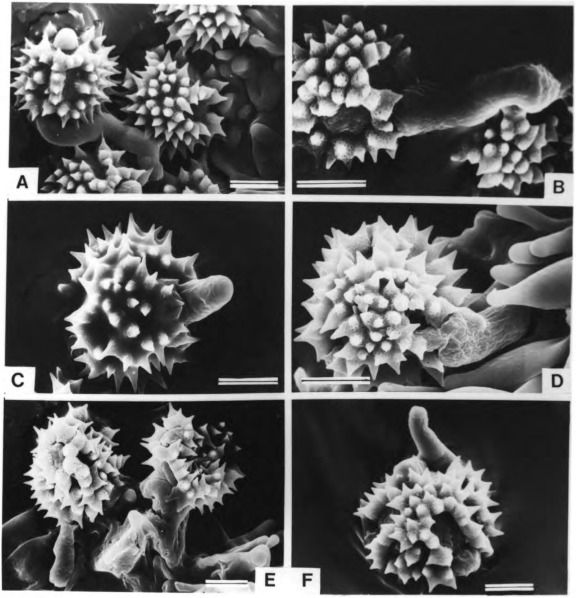


Figure 18

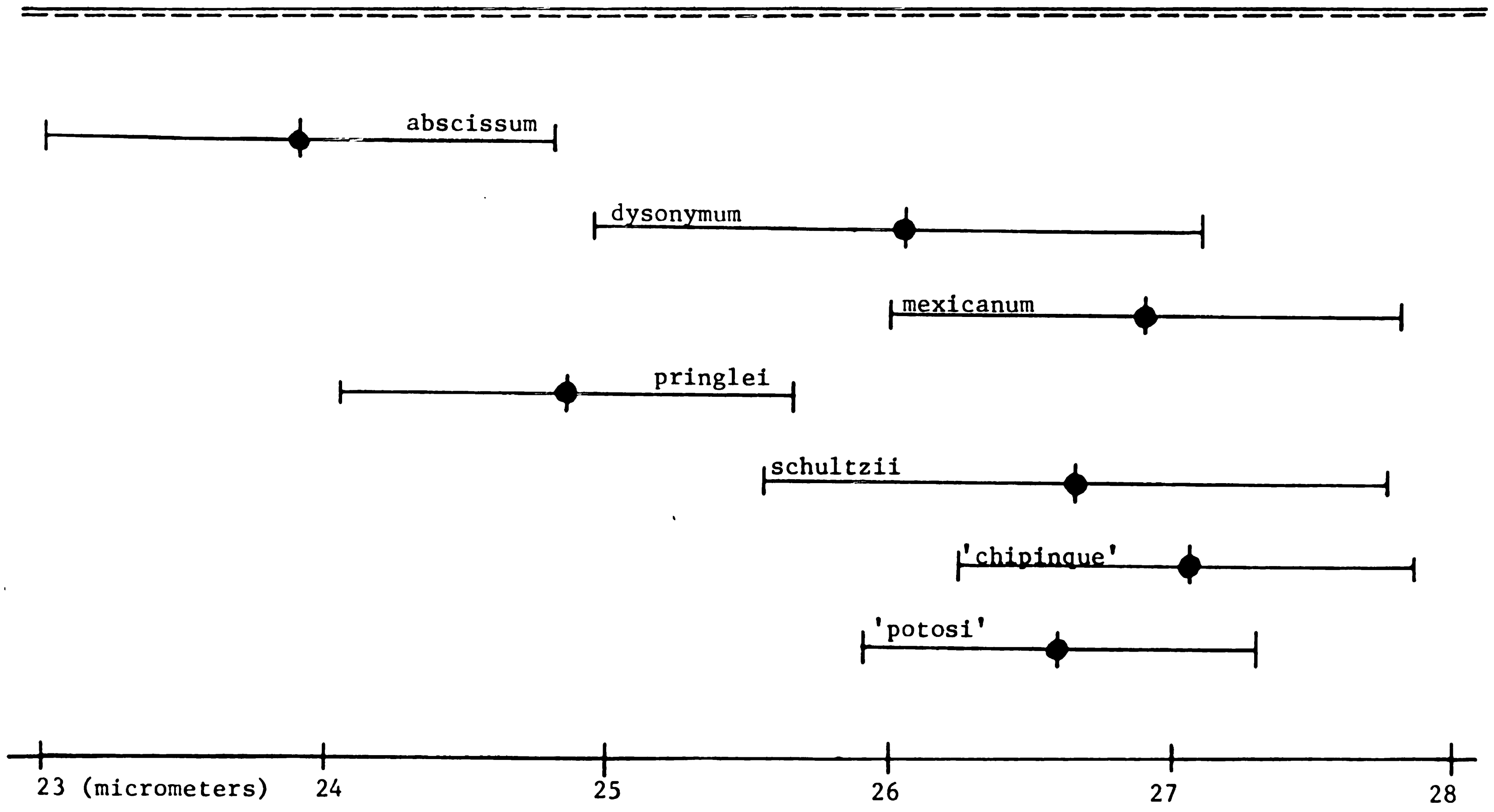
Table 17. Evaluations of species of Mexican <u>Hieracium</u> pollen grains based on scanning electron micrographs. All measurements in micrometers.

Species	Soule Coll. number	Diameter	# of spines/ pore	# of spines/ lacuna	spine geometry	overall spine length	length above pits	% spine above pits
H. abscissum	1573	23.636	10	—	c	5.455	2.727	49.99
H. abscissum	1573	—	10	--	c	8.182	4.091	50.00
H. abscissum	1559	25.455	--	—	c	—	---	---
H. abscissum	1559	26.364	—	12	c	—	---	---
H. abscissum	1559	25.455	--	12	c	—	---	---
H. abscissum	1654	21.000	—	—	c	—	---	---
H. abscissum	1654	21.667	--	12	c	—	---	---
	Average	23.929	10	12	c	6.819	3.409	49.99
	S.E.	0.901						
H. dysonymum	1412	28.333	--	—	s	---	---	---
H. dysonymum	1412	27.500	--	—	s	---	---	---
H. dysonymum	1550	24.000	10	8	s	4.000	2.000	50.00
H. dysonymum	1586	22.667	--	8	s	---	---	---
H. dysonymum	1586	27.778	--	8	s	4.444	2.222	50.00
	Average	26.056	10	8	s	4.222	2.111	50.00
	S.E.	1.14						
H. mexicanum	1593	—	--	8	s	—	---	---
H. mexicanum	1593	—	--	8	s	—	---	---
H. mexicanum	1593	23.500	12	8	s	4.000	2.000	50.00
H. mexicanum	1594	—	--	—	s	5.556	3.333	59.98
H. mexicanum	1604	30.000	12	10	s	5.000	2.222	44.44
H. mexicanum	1604	—	--	--	s	5.556	3.333	59.98
H. mexicanum	1605	29.333	12	10	s	4.667	2.667	57.15
H. mexicanum	1605	—	12	10	s	---	---	---
H. mexicanum	1605	27.220	--	—	s	5.556	2.778	50.00
H. mexicanum	1612	29.333	12	10	s	5.333	2.667	50.01
H. mexicanum	1612	25.556	--	—	s	4.444	2.667	37.51
H. mexicanum	1612	23.889	--	—	s	---	---	---
H. mexicanum	1629	26.111	--	10	s	5.000	3.333	66.66
	Average	26.867	12	10 or 8	s	5.012	2.667	52.86
	S.E.	0.892						

Table 17 (continued). Evaluations of species of Mexican Hieracium pollen grains based on scanning electron micrographs. All measurements in micrometers.

Species	Soule Coll. number	Dia- meter	# of spines/ pore	# of spines/ lacuna	spine geo- metry	overall spine length	length above pits	% spine above pits
H. pringlei	1516	25.00	10	8	s	---	---	---
H. pringlei	1516	27.50	--	---	s	---	---	---
H. pringlei	1516	22.73	---	8	s	4.545	2.045	44.99
H. pringlei	1516	---	10	8	s	6.000	2.000	33.33
H. pringlei	1516	---	--	---	s	6.000	2.500	41.67
H. pringlei	1519	24.06	---	8	s	---	---	---
H. pringlei	1579	25.00	10	8	s	4.000	2.000	50.00
	Average	24.86	10	8	s	5.136	2.136	42.50
	S.E.	0.783						
H. schultzii	1409	25.56	12	---	c	5.56	3.33	59.98
H. schultzii	1409	27.22	--	---	c	---	---	---
	Average	26.66	12	---	c	5.56	3.33	59.98
	S.E.	1.103						
H. 'chipinque'	1696	26.36	10	--	c	5.45	3.64	66.79
H. 'chipinque'	1696	28.18	10	12	c	3.64	2.73	75.00
H. 'chipinque'	1696	26.36	--	12	c	3.64	2.73	75.00
H. 'chipinque'	1696	29.44	10	12	c	---	---	---
H. 'chipinque'	1696	25.00	10	12	c	4.00	2.00	50.00
	Average	27.07	10	12	c	4.20	2.78	66.70
		0.778						
H. 'potosi'	1507	28.000	--	8	s	4.666	2.000	42.91
H. 'potosi'	1507	---	--	8	s	---	---	---
H. 'potosi'	1513	26.154	10	--	s	3.846	---	---
H. 'potosi'	1513	28.421	--	8	s	---	---	---
H. 'potosi'	1513	25.000	10	8	s	---	---	---
	Average	26.592	10	8	s	4.256	2.000	42.91
	S.E.	0.6896						

Figure 19. Average size of *Hieracium* pollen grains by taxa. Circle denotes average, bar indicates ± standard error.



each germinal pore. Terms used are defined by Erdtman (1954). Overall grain diameter was recorded. The average and standard error for the diameter of each taxon was determined (Table 17 and Figure 19).

In general overall pollen diameter cannot be used to distinguish species in this group. The differences in pollen size between members of a single species may be due to differential energy expenditure by the pollen parent as demonstrated in the work by Bell (1959), or it may represent an actual taxon-related character. A larger sample size is needed to make a definitive statement.

Total length of the spines and the percentage of spine above the pits was determined. The spines are pitted on the lower 42 to 60 percent of the spine. The amount of extension of the spine above the pits could not be used to distinguish species. It should be mentioned that the presence of such prominent spines is indicative of an insect pollinated as opposed to a wind pollinated group (Grashoff and Beaman 1970).

The most taxon-specific character was the number of spines on the annulus and around the lacuna. *Hieracium abscissum* consistently had 10 spines per annulus and 12 per lacuna as did *H.* '*chipinque*.' *Hieracium dysonymum* and *H.* '*potosi*' had 10 and 8 as did *H. pringlei*. *Hieracium mexicanum* spines numbered 12 and 10 or 8, and *H. schultzii* had 12 annular spines.

A surprising discovery was that germinated pollen was found on all stubs to which stigmatic tissue had adhered (Figure 18). Stubs lacking stigmatic tissue had no germinated pollen. Although there can be some criticism of utilizing field-collected pollen (possible contamination by pollen of other species), the unexpected discovery of germinated pollen provided the benefit of knowing that at least some of the pollen was viable.

Observation showed that on almost all stubs no malformed, collapsed, or significantly smaller pollen grains were observed. This fact combined with the evidence of viable, germinated pollen suggest that the species examined in this study are not apomictic. The light microscopy studies of Beaman (1957) and Grashoff (1969) on other apomictic New World Compositae found a high number of malformed, collapsed, or significantly smaller pollen grains. One might expect to find this result in Mexican *Hieracium* as well. It might also be reasonable to expect that one would not find a proliferation of germinated pollen in the case of apomicts.

Conclusions

The Mexican species of *Hieracium* investigated can be separated into two groups based on pollen morphology, the "curved-spine" group and the "straight-spine" group, as seen in Figure 17. The two groups correspond with growth form. The many headed species — *Hieracium abscissum*, *H. schultzii*, and *H. 'chipinque,'* have curved spines; the few headed species -- *H. dysonymum*, *H. mexicanum*, *H. pringlei*, and *H. 'potosi,'* have straight spines.

The number of annular and lacunar spines proved species constant and provides evidence for not recognizing *Hieracium 'chipinque'* and *H. 'potosi'* as separate taxa since these pollen characters correspond to those of *H. abscissum* and *H. dysonymum* respectively.

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APPENDICES

APPENDIX I

Citation of specimens used in the compilation of distribution maps.

Hieracium abscissum

Chiapas: Zinacantan, ridge between paraje of Nachih & Zinacantan Center. 2350 m elev. *Breedlove 39793* (MO, TEX).

Distrito Federal: N side of Cerro Ajusco. 19° 13'N; 99° 15'W. 3150 m elev. *Beaman 5123* (MSC).

Durango: Km 32 on Hiway 40 W of Durango, steep slope E side of road. Scattered oaks. *Warnock 2166* (TEX).

Guerrero: Municipio Chichihualco. Asoleadero, ca. 15 km W of Camotla. Pine-fir forest. 2650 m elev. *Feddewa 2836* (TEX).

Hidalgo: Cerro de las Ventanas, El Chico National Park. 20° 13'N; 98° 45'W. Fir forest. 2900 m elev. *Beaman 5114* (MSC).

Jalisco: NW slopes of Nevado de Colima. Spruce-fir zone. 2450 m elev. *McVaugh 10099* (MEXU).

Mexico: Valle de Bravo. Pine forest. 2000 m elev. *Boege 1751* (MEXU).

Mexico: 3.8 mi W of border between Puebla and Mexico, on free road. Hillside S face of mts. near the summit of Llano Grande pass of the Sierra de Rio Frio. Pines. 3150 m elev. *Soule 1675* (MSC).

Michoacan: Municipio Coalcoman, Barreloso. Cornfield. 2300 m elev. *Hinton 15088* (TEX, MO).

Nayarit: 51 mi NW of Tepic on Hiway 15. Wet marsh soil, coastal plain. *Jackson 7199* (TEX).

Nuevo Leon: Crest of Sierra Madre Oriental between Zaragosa & Siberia, E of Pena Nevada. Oak forest. 2700 m elev. *Beaman 6631* (MSC).

Nuevo Leon: Cerro Pena Nevada, ca. 12 km NE of San Antonio Pena Nevada; 30 km E of Dr. Arroyo. *Wells 317* (TEX).

Nuevo Leon: Sierra La Marta, Galeana. Fir-spruce woods. 3150 m elev. *Hinton 18315* (TEX).

Nuevo Leon: Infiernillo to SW of Galeana near La Cima; Sierra Madre Oriental. 3000 m elev. No collector listed (MEXU).

Nuevo Leon: Sierra Madre Oriental near Monterrey. *Pringle 13853* (TEX).

Oaxaca: 14 mi E of Ixtlan. 2900 m elev. *Beaman 6498* (MSC).

Oaxaca: Mountains, ca. 48 road mi N of Oaxaca and 17 road mi S of pass between Oaxaca and Tuxtepec. 9300 m elev. *Cronquist 9656* (MEXU, TEX).

Puebla: 4.8 mi NE of Honey. 20° 15'N; 98° 25' W. Pine forest. 1700 m elev. *Beaman 6497* (MSC).

Puebla: 2.2 mi S of the border between Puebla and Mexico, on the free road to Mexico City. Steep road cut in pine forest. 2800 m elev. *Soule 1668* (MSC).

Puebla: 0.4 mi S of the border between Puebla and Mexico, on the free road to Mexico City. In a state run tree nursery. Pines and oaks with bunch-grasses. 3000 m elev. *Soule 1671* (MSC).

Queretaro: 23.2 mi past Jalpan on Hiway 120 to San Juan del Rio. N to NW facing 80-90° road cuts. *Quercus*, *Pinus*, cultivation. 2200 m elev. *Soule 1559* (MSC).

Queretaro: 27.9 mi past Jalpan on Hiway 120 to San Juan del Rio. In planted pine forest, 30-45° slope facing E. Just at the top of the pass; *Pinus*, few *Quercus*. 2600 m elev. *Soule 1561* (MSC).

Queretaro: Ca. 0.5 mi N of Amelco on Hiway 120. Series of water tanks made of soil, banks ungrazed. *Soule 1572* (MSC).

San Luis Potosi: Near Puerta de Huerta, Sierra de Alvarez. 22° 08'N; 100° 47' W. Low oak forest. 2300 m elev. *Beaman 5113* (MSC).

Veracruz: 4.0 mi from route 140 down the road to Misantla in mal pais (old lava flow). *Pinus pseudostrobus*. 1450 m elev. *Soule 1638* (MSC).

Veracruz: 12.1 mi from route 140 down the road to Misantla. Steep, ungrazed 70-80° E facing cut. *Alnus*, *Quercus*, *Toxicodendron*. 1650 m elev. *Soule 1648* (MSC).

Veracruz: 21.1 mi towards Misantla from Hiway 140 to Xalapa. Plants growing in cow pasture and along steep road cut. 2100 m elev. *Soule 1651* (MSC).

Veracruz: 13.7 mi towards Puebla on Hiway 140 from Xalapa. Plants growing under pines in mal pais (old lava flow). *Quercus* and *Pinus*. 2350 m elev. *Soule 1654* (MSC).

Veracruz: 13.7 mi towards Puebla on Hiway 140 from Xalapa. Plants growing under pines in mal pais (old lava flow). 2350 m elev. Soule 1655 (MSC).

Veracruz: 19.2 mi towards Puebla on Hiway 140 from Xalapa. Plants growing under pines. 2350 m elev. Soule 1657 (MSC).

Veracruz: 19.2 mi towards Puebla on Hiway 140 from Xalapa. Plants growing under pines. 1650 m elev. Soule 1658 (MSC).

Veracruz: 10 mi S of Orizaba, road to Zongolica. Hill overlooking Aquila. 18° 41'N; 97° 04'W. 2000 m elev. Turner 15308 (TEX).

Hieracium dysonymum

Distrito Federal: Extreme SW of the Pedregal de San Angel. 2800 m elev. Rzedowski 34698 (ASUF).

Distrito Federal: Monte Alegre, Serrania del Ajusco, Delegacion de Tlalpan. 3400 m elev. Rzedowski 37667 (MEXU).

Distrito Federal: Capulticla San Bernabe, delegacion Contreras. "Bosque de oyamel." 2800 m elev. Ventura 2645 (MEXU, TEX).

Durango: Km 65 on Route 40 W of Durango. Scattered pines. Warnock 2164 (TEX).

Guerrero: Cerro Teotepec, Municipio Tlacotepec. Pine-fir forest with grasses. 3200 m elev. Rzedowski 18553 (MICH, TEX).

Mexico: At Km 15 between Amecameca and Paso de Cortes. 19° 05' N; 98° 40' W. 3200 m elev. Beaman 5124 (MSC).

Mexico: 12 km E of Amecameca, on the road to Tlamacas. "Ladera andesitica con vegetacion de bosque de Abies." 3100 m elev. Rzedowski 35593 (MEXU).

Mexico: Side of road 0.5 mi past border with Michoacan. Plants in ungrazed road cuts at the sides of the road. Pine-spruce forest. 2850 m elev. Soule 1586 (MSC).

Michoacan: N and S slopes of Mt. Tancitaro. Open pine forest. 10,000 ft elev. Leavenworth & Hoogstraal 1137 (MO).

Michoacan: Road cut on steep slopes above Laguna Larga. San Andres Mountains, steep 75-90° slope NW facing. Pines. 2875 m elev. Soule 1583 (MSC).

Michoacan: Road cut next to Laguna Larga. San Andres Mountains. Pines. 2800 m elev. Soule 1582 (MSC).

Nuevo Leon: Sierra La Marta, on a limestone ridge. 3400m elev. Hinton 18317 (ARIZ, TEX).

Nuevo Leon: San Francisco Canyon, ca. 15 mi SW of Pueblo Galeana. 7500-8000 ft elev. Mueller 415 (MICH).

Nuevo Leon: Ascent to Sierra Infernillo, ca. 15 mi SW of Galeana. 9000-10,000 ft elev. Mueller 826 (MICH).

Nuevo Leon: 2.7 mi below the top of Cerro Potosi. In dense numbers under one pine. 3500 m elev. Soule 1507 (MSC).

Nuevo Leon: Road up to the top of Cerro Potosi, ca. 8 mi below the radio towers at the top. Mesic meadow with pines, few oaks. 2950 m elev. Soule 1501 (MSC).

Nuevo Leon: 1.5 mi below the top of Cerro Potosi. 3550 m elev. Soule 1503 (MSC).

Nuevo Leon: Cerro Potosi, 3.5 mi below the summit. Plants in bud, no flowers. Plants mostly around rocky outcrops where slightly more mesic. 3425 m elev. Soule 1510 (MSC).

Nuevo Leon: Cerro Potosi, 4.9 mi below the summit. SE facing slope of 30°. Plants mostly in part shade under pines. 3325 m elev. Soule 1513 (MSC).

Nuevo Leon: Mt. Picacho Onofre, ca. 12 km NE of San Antonio Pene Nevada; 30 mi E of Dr. Arroyo. Wells 401 (TEX).

Oaxaca: Ca. 14 mi E of Ixtlan. 2900 m elev. Beaman 6499 (MSC).

Oaxaca: Near Buena Vista, ca. 8 km E of Paso de Cortez. *Pinus hartwegii* forest. 3350 m elev. Beaman 6666 (MSC).

Oaxaca: Between Ixtlan de Juarez and Llano de los Flores. 2600 m elev. Beaman 6679 (MSC).

Puebla: 1.2 mi W of Texmalquila, just SE of Pico de Orizaba. Pine, fir, alder, *Senecio*. 10-11,000 ft elev. Lento 21926 (ASUF).

Puebla: 11.5 mi from Paso de Cortes Monument, down the back of Popocatepetl and Iztaccihuatl on the dirt road. On sides of steep road cut. Pine-oak. 3300 m elev. Soule 1627 (MSC).

Queretaro: 15.5 mi past Jalpan Hiway 120 to San Juan del Rio. N to NW facing 80-90° road cuts. 1500 m elev. Soule 1558 (MSC).

San Luis Potosi: 55 mi NW of Rio Verde on Hiway 70 to San Luis Potosi. In full sun next to road, or under pines above road in ungrazed areas. 2450 m elev. Soule 1550 (MSC).

Tamaulipas: Sierra de San Carlos, vicinity of San Jose; above La Vegonia. 3300 ft elev. Bartlet 10055 (MICH).

Tamaulipas: Santa Rita Ranch. 1500 m elev. Runyon 847 (TEX).

Tamaulipas: E and S slopes of Pena Nevada. Stanford 2564 (MICH).

Veracruz: 7.2 mi from the town of Perote down a side road from the road up the Cofre. Flat areas under Pinus and Alnus. 3100 m elev. Soule 1636 (MSC).

Veracruz: 11.5 mi from the town of Perote on the road up to the Cofre. N facing 5-10° slope. Pines and bunch-grass. 3550 m elev. Soule 1633 (MSC).

Veracruz: Under pines on hillside outside of Villa Aldama. 2650 m elev. Soule 1660 (MSC).

Hieracium mexicanum

Distrito Federal: N side of Cerro Ajusco, 19° 13' N; 99° 15' W. 3250 m elev. Beaman 5121 (MSC).

Guerrero: Cerro Teotepec, Tlacotepec. "Bosque abierto de Pinus y Abies con gramineas." 3200 m elev. Rzedowski 18553 (MEXU).

Jalisco: 19 km S of Talpa along the road to La Cuesta. Pine forest. 1400 m elev. Hernandez & Delgado 1331 (MEXU, TEX).

Mexico: 18 km towards Texcoco, Municipio Tepetlaxatoc. Near the border with Tlaxcala. 2870 m elev. Garcia 1693 (TEX).

Mexico: Mountains N of Huehuetoca, near the border of Hidalgo, ca. 2400 m elev. Gold 21749 (MEXU).

Mexico: Ca. 4 mi up the road to the top of Nevado de Toluca, down a dirt side road. Pine forest with bunch-grasses, 3700 m elev. Soule 1590 (MSC).

Mexico: Ca. 1/2 mi up the road to the top of Nevado de Toluca. Pine forest with bunch-grasses, 3520 m elev. Soule 1593 (MSC).

Mexico: Ca. 1/2 mi up the road to the top of Nevado de Toluca. Pine forest with bunch-grasses, 3520 m elev. Soule 1594 (MSC).

Mexico: Ca. 1/2 mi from Paso de Cortez on dirt road that goes down the back of Popocatepetl and Iztaccihuatl. Pines and bunch-grass cover the steep slope. 3600 m elev. Soule 1604 (MSC).

Mexico: Ca. 1/2 mi from Paso de Cortez on dirt road that goes down the back of Popocatepetl and Iztaccihuatl. Pines and bunch-grass cover the steep slope. 3600 m elev. Soule 1605 (MSC).

Mexico: 2 mi along the road to Iztaccihuatl trail from the Paso de Cortez monument. E facing slope. Pines and bunch-grass. 3790 m elev. *Soule 1611* (MSC).

Mexico: 2.7 mi along the road to Iztaccihuatl trail from the Paso de Cortez monument. E facing slope. Pines and bunch-grass. 3800 m elev. *Soule 1612* (MSC).

Mexico: End of road at the base of the trail up Iztaccihuatl. Above timberline. N facing slope. Bunch-grasses cover the slope. 4000 m elev. *Soule 1614* (MSC).

Mexico: 3.8 mi W of border between Puebla and Mexico, on free road. Hillside, S face of mts. near the summit of Llano Grande pass of the Sierra de Rio Frio. Pines. 3150 m elev. *Soule 1676* (MSC).

Mexico: 5.3 mi W of border between Puebla and Mexico, on free road. Hillside, S face of mts. at the summit of Llano Grande pass of the Sierra de Rio Frio. *Pinus*, *Quercus*. 3275 m elev. *Soule 1678* (MSC).

Mexico: 5.3 mi W of border between Puebla and Mexico, on free road. Hillside S face of mts. at the summit of Llano Grande pass of the Sierra de Rio Frio. *Pinus*, *Quercus*. 3275 m elev. *Soule 1679* (MSC).

Mexico: Nevado de Toluca, just below timberline, below the dirt road to the top. Pines and bunch-grasses. 4000 m elev. *Soule 1681* (MSC).

Michoacan: Summit of Cerro San Andres, ca. 12 km (straight line distance) N of Ciudad Hidalgo. 3589 m elev. *Beaman 4287* (MSC).

Puebla: Pico de Orizaba, SW side of the mountain. 3860 m elev. *Beaman 2516* (MSC).

Puebla: Lado Norte de Pinal, entre rocas con *Pinus oaxacana* y *P. teocote*. 2800 m elev. *Boege 2137* (MEXU).

Puebla: Pico de Orizaba. 11-12,000 ft elev. *Pringle 8550* (MEXU, MO, MSC, TEX).

Puebla: 9.9 mi from Paso de Cortez monument, down the back of Popocatepetl and Iztaccihuatl, dirt road. Pine forest, few bunch-grasses. 3450 m elev. *Soule 1620* (MSC).

Veracruz: 6.3 mi from the town of Perote on the road up Cofre de Perote. Planted pines. 3050 m elev. *Soule 1629* (MSC).

Veracruz: 6.3 mi from the town of Perote on the road up Cofre de Perote. Planted pines. 3050m elev. *Soule 1630* (MSC).

Veracruz: 11.5 mi from the town of Perote on the road up to the Cofre. N facing 5-10° slope. Pines and bunch-grass. 3550 m elev. *Soule 1632* (MSC).

Hieracium pringlei

Agua Caliente: Sierra del Laurel near the border to Jalisco, ca. 10 mi. SE of Calrillo. Oak forests near summit. 2600 m elev. *McVaugh 18450* (MICH).

Chiapas: Clinica Yerba Buena, 2 km NW of Pueblo Nuevo Solistahacan. Chromosome voucher. Pine-oak-sweetgum. 5400 ft. elev. *Breedlove* and *Raven 19921* (MICH).

Chiapas: Near Piedracitos, ca. 7 km E of San Cristobal las Casas. Oak-pine forest. 7200 ft. elev. *Breedlove 8006* (MICH).

Chihuahua: Basaseachic Falls area. 6400 ft. elev. *Pinkava 13265* (ASUF).

Chihuahua: La Bufa above Cusihuiriacha. *Pringle 1585* (MEXU, MICH, MO, MSC).

Coahuila: Sierra Santa Fe del Pino, 28° 12' N; 103° 03' W. Juniper-oak forest. 2100 m elev. *Johnston 11255* (TEX).

Distrito Federal: Base of Sierra de Ajusco. 2400 m elev. *Pringle 7211* (MO, MSC, TEX).

Distrito Federal: N of Cerro de Santa Catarina, around Santa Marta Astahuacan. 2500 m elev. *Rzedowski 30821* (MSC).

Durango: 32.7 mi W of Durango on creek terraces. Pine-oak Forest. *Johnston 2693* (TEX).

Guanajuato: 8 km NE of Santa Rosa. 2400 m elev. *McVaugh 24113* (MICH).

Jalisco: Nevado de Colima. 3070 m elev. *Eiten* & *Gregory 289* (MICH).

Jalisco: Cerro de Talcozagua, on Sierra de Tapalpa, 2-3 km E of Tapalpa. 19° 57'N; 103° 45'W. 2000 m elev. *Iltis et al. 754* (MICH).

Jalisco: Sierra de Cuale, SW of Talya de Allende. Pine forest. 2200 m elev. *McVaugh 14262* (MICH).

Jalisco: Las Vidrieas, 10 km NW of El Platanar, Municipio San Martin de Bolanos. 2450 m elev. *Rzedowski 26181* (MICH).

Jalisco: Rincon de Manantlan. 19° 33' 30" N; 104° 13' 15" W. Cloud forest. 2250 m elev. *Sorensen 7884* (MICH).

Jalisco: Volcan Colli, Sierra de la Venta, 10 km W of Guadalajara. *Villareal 4649* (MICH).

Jalisco: Mountains E of Mamantlan, ca. 15 mi SSE of Antlan via Chante. 8300 ft elev. *Wilbur 1803* (MICH).

Michoacan: Vicinity of Morelia. 2100 m elev. Arsene 6626 (MO).

Michoacan: Logging road 24 miles past border with Michoacan. E facing slope. Pine-oak forest. 2440 m elev. Soule 1575 (MSC).

Michoacan: Logging road 24 miles past border with Michoacan. E facing slope. Pine-oak forest. 2440 m elev. Soule 1576 (MSC).

Michoacan: Ca. 10.5 mi past the border with Mexico. 70° E facing slope very wet, lots of moss, liverworts. On cut and in pine-oak forest. 2390 m elev. Soule 1577 (MSC).

Michoacan: Ca. 10.5 mi past the border with Mexico. 70° E facing slope, dry, sandy soil. Pine-oak forest. 2390 m elev. Soule 1578 (MSC).

Michoacan: 4.8 mi down road to Los Azufres off Hiway 15. Slopes of 0-45° facing all directions, ungrazed. Pine-oak forest. 2425 m elev. Soule 1579 (MSC).

Nuevo Leon: Ca. 13 km SSE of Galeana Santa Rita. 1980 m elev. Hinton 18300 (TEX).

Nuevo Leon: Galeana, Sierra La Marta. 3400 m elev. Hinton 18317 (ASUF).

Nuevo Leon: Dulces Nombres, just E of border with Tamaulipas. Oak forest. 1950 m elev. Meyer 2620 (MO).

Nuevo Leon: On Highway 51 (road to Dr. Arroyo) 5.6 mi S of junction of Hw 51 & Hw 58. Dry canyon with pinyon pines. 6400 ft. elev. Smith 2103 (TEX).

Nuevo Leon: 68 mi N of Zaragosa on gypsum soil with pockets of high OM under pinyon pines. 10° NE facing slope. 2000 m elev. Soule 1516 (MSC).

Nuevo Leon: 68 mi N of Zaragosa on gypsum soil with pockets of high OM under other plants. 30° NE facing slope. Pines. 2000 m elev. Soule 1519 (MSC).

Nuevo Leon: 68 mi N of Zaragosa on gypsum soil with pockets of high OM under other plants. 30° NE facing slope. Pines. 2000 m elev. Soule 1520 (MSC).

Nuevo Leon: 65 mi N of Zaragosa on gypsum soil with pockets of high OM under pinyon pines. E facing 5-10° slope. Pinyon pine, juniper. 2125 m elev. Soule 1523 (MSC).

Nuevo Leon: 61 mi N of Zaragosa. Gypsum soil with pockets of high OM under pinyon pines. 5-35° slope facing NW to W to SW. Above road only. Pinyon pine, juniper, manzanita. 2225 m elev. Soule 1524 (MSC).

Puebla: Cerro de Gentile. 7000-8000 ft elev. Purpus 3848 (MO).

Puebla: On La Derrumbada (landslide hill), uncultivated hill on the west side of the road to Guadalupe Victoria off Hiway 140. Municipio de Guadalupe Victoria. Pines, oaks, and agaves. 2600 m elev. Soule 1665 (MSC).

Puebla: On La Derrumbada (landslide hill), uncultivated hill on the west side of the road to Guadalupe Victoria off Hiway 140. Municipio de Guadalupe Victoria. Pines, oaks, and agave. 2600 m elev. Soule 1666 (MSC).

Queretaro: Cerro Zamorano, 1 km SW of Cumbre. Spruce forest. 3100 m elev. McVaugh 402 (MICH).

San Luis Potosi: Near San Luis Potosi. 7000 ft. elev. Parry & Palmer 552 (MO).

Tamaulipas: Pico del Diablo, vicinity of Marmolejo. Bartlett 10909 (MICH).

Veracruz: 4.0 mi from route 140 down the road to Misantla in mal pais (old lava flow). Pinus pseudostrobus. 1450 m elev. Soule 1639 (MSC).

Veracruz: Under pines on hillside outside of Villa Aldama. 2650 m elev. Soule 1659 (MSC).

Veracruz: Under pines on hillside outside of Villa Aldama. 2650 m elev. Soule 1660 (MSC).

Zacatecas: Ca. 20 km W towards Tlaltenango from road junction S of Julpa. Oak-pine forest. 2400 m elev. McVaugh 25631 (MICH).

Hieracium schultzii

Chihuahua: Hills near Chihuahua. Pringle 771 (MSC).

Coahuila: 17 km N of Rio El Jardin, 29° 10' N; 102° 46'W. Pinyon pines. Johnson 11900 (TEX).

Distrito Federal: Desierto de los Leones. Lyonnet 407 (MO).

Durango: City of Durango and vicinity. Palmer 653 (MO).

Durango: San Juan de Michis, al cerro "chihuahullia." Chavez 50 (TEX).

Hidalgo: Tepeapulco. 2550 m elev. Ventura 1515 (ARIZ, ASUF, XAL).

Mexico: 13.3 mi down the road to Valle de Bravo, road that is closer to Toluca, but not from Toluca. W facing cut. 2810 m elev. Soule 1588 (MSC).

Mexico: 6 km W of San Cristobal Ecatepec, parte alta de la Sierra de Guadalupe. Vegetacion de matorral. 2600 m elev. *Rzedowski 32166* (MEXU, MSC, XAL).

Mexico: 8 km E of Coatlinchan. 2250 m elev. *Rzedowski 35148* (MEXU, MSC).

Mexico: Parte SE del Cerro del Pino. 2600 m elev. *Rzedowski 34801* (MEXU, MSC, XAL).

Mexico: Valley of Mexico, Pedregal. *Bourgeau s.n.* (MSC).

Oaxaca: S slope of El Pasajuego, ca. 25 km NE of Oaxaca on Hiway 175. Oak-pine forest. 2000-3000 m elev. *Conrall 3085* (MEXU).

Oaxaca: Sierra de San Felipe. 10,000 ft elev. *Pringle 4715* (MEXU).

Pueblo: Hills near Amozoc. 9000 ft elev. *Pringle 9360* (MO).

Pueblo: San Luis Tultitlanapa, near Oaxaca. *Purpus 3131* (MO).

Queretaro: Ca. 0.5 mi N of Amelco on Hiway 120. Series of water tanks made of soil, banks ungrazed. *Soule 1572* (MSC).

San Luis Potosi: 55 mi NW of Rio Verde on Hiway 70 to San Luis Potosi. Under pines above road, or in full sun next to road, in ungrazed area. 2450 m elev. *Soule 1551* (MSC).

San Luis Potosi: Cheifly in the region of San Luis Potosi, 22° N. 6000-8000 ft elev. *Parry 553* (MO).

San Luis Potosi: Microwave hill about 15 mi SE of San Luis Potosi. In road cut at base of hill. N facing slope to 70°. 2500 m elev. *Soule 1549* (MSC).

Veracruz: 14 km NE of Huayacocotla, 20° 36' N; 98° 28' W. 1650 m elev. *Vasques 50* (XAL).

Veracruz: Under pines on hillside outside of Villa Aldama. 2650 m elev. *Soule 1661* (MSC).

Zacatecas: 16 mi E of Concepcion del Oro, on upper N side of Sierra del Astillero, 24° 38' N; 101° 08' W. 8200 ft elev. *Hendrickson 13342* (TEX).

APPENDIX II

Raw data used in statistical analysis of the vestiture.

The presence or absence of each type of vestiture was established after all SEM work was completed and the resulting micrographs surveyed. The results were scored and entered in a data matrix for statistical analysis using MVSP (see text). This matrix is presented below.

Scoring evaluated the presence of a character as 0.99, absence of the character as 0.01. Lengths of glandular hairs were measured and their average entered. Barb lengths were evaluated and long barbs (see text) were scored at 0.99, short barbs at 0.01. Rows consisted of each sample and its characters, columns were determined by the following categories:

c0 species combined with collection number to define each row, limited to eight characters, printed out but not recognized for analysis by the program,
c1 phyllary—stellate hairs,
c2 phyllary--glandular hairs,
c3 phyllary--barbed hairs,
c4 phyllary--waxes,
c5 stem below the head--glandular hairs,
c6 stem below the head--stellate hairs,
c7 stem below the head--barbed hairs,
c8 stem below the head--waxes,

c9 upper surface of the leaves--glandular hairs,

c10 upper surface of the leaf--stellate hairs,

c11 upper surface of the leaf--barbed hairs,

c12 upper surface of the leaf--barb length,

c13 upper surface of the leaf--waxes,

c14 lower surface of the leaf--glandular hairs,

c15 lower surface of the leaf--stellate hairs,

c16 lower surface of the leaf--barbed hairs,

c17 lower surface of the leaf--barb length,

c18 lower surface of the leaf--waxes,

c19 stem at the base of the plant--glandular hairs,

c20 stem at the base of the plant--stellate hairs,

c21 stem at the base of the plant--barbed hairs,

c22 stem at the base of the plant--barb length,

c23 stem at the base of the plant--waxes,

c24 pappus color white,

c25 pappus color tawny,

c26 leaves basal only,

c27 leaves basal and cauline.

Data matrix used for MVSP statistical analysis (see text).

	c1	c2	c3	c4	c5	c6	c7	c8	c9	c10	c11	c12	c13	c14	c15	c16	c17	c18	c19	c20	c21	c22	c23	c24	c25	c26	c27
abs1408	0.99	0.50	0.01	0.99	0.99	0.99	0.01	0.99	0.01	0.01	0.80	0.01	0.99	0.01	0.01	0.90	0.01	0.99	0.01	0.01	0.99	0.01	0.99	0.01	0.99	0.01	0.99
abs1573	0.99	0.30	0.01	0.99	0.30	0.99	0.01	0.99	0.01	0.01	1.20	0.01	0.99	0.01	0.01	1.50	0.01	0.99	0.01	0.01	0.99	0.01	0.99	0.01	0.99	0.01	0.99
abs1648	0.99	0.20	0.01	0.99	0.20	0.99	0.01	0.99	0.01	0.01	1.00	0.01	0.99	0.01	0.01	1.25	0.01	0.99	0.01	0.01	0.99	0.01	0.99	0.01	0.99	0.01	0.99
dys1412	0.99	0.30	0.01	0.01	0.01	0.99	0.01	0.01	0.99	0.01	1.50	0.01	0.01	0.99	0.01	1.25	0.01	0.01	0.99	0.01	0.99	0.01	0.01	0.01	0.99	0.01	0.99
dys1421	0.99	0.57	0.01	0.01	0.01	0.99	0.01	0.01	0.99	0.01	1.50	0.01	0.01	0.99	0.99	1.25	0.01	0.01	0.99	0.01	0.99	0.01	0.01	0.01	0.99	0.01	0.99
dys1550	0.99	0.39	0.01	0.01	0.20	0.99	0.01	0.01	0.01	0.01	1.50	0.01	0.99	0.01	0.01	1.25	0.01	0.99	0.01	0.01	0.99	0.01	0.01	0.01	0.99	0.01	0.99
mex1420	0.99	0.13	0.99	0.01	0.26	0.99	0.01	0.01	0.99	0.99	0.99	0.01	0.01	0.99	0.99	1.25	0.01	0.01	0.99	0.99	0.99	0.01	0.01	0.99	0.01	0.99	0.01
mex1593	0.99	0.15	0.99	0.01	0.18	0.99	0.50	0.01	0.99	0.01	0.99	0.01	0.01	0.01	0.01	1.25	0.01	0.01	0.99	0.99	0.99	0.01	0.01	0.99	0.01	0.99	0.01
mex1614	0.99	0.01	0.99	0.01	0.18	0.99	0.99	0.01	0.01	0.01	0.99	0.01	0.01	0.01	0.01	1.25	0.01	0.01	0.99	0.99	0.99	0.01	0.01	0.99	0.01	0.99	0.01
pri1575	0.99	0.80	0.01	0.99	0.40	0.99	0.01	0.99	0.01	0.01	1.50	0.99	0.99	0.01	0.01	1.50	0.99	0.99	0.01	0.01	0.99	0.99	0.01	0.01	0.99	0.01	0.99
pri1664	0.99	1.20	0.01	0.99	0.50	0.99	0.01	0.99	0.01	0.01	1.70	0.99	0.99	0.01	0.01	1.50	0.99	0.99	0.01	0.01	0.99	0.99	0.01	0.01	0.99	0.01	0.99
pr30821	0.99	0.28	0.01	0.99	0.27	0.99	1.00	0.99	0.01	0.01	1.50	0.99	0.99	0.01	0.01	2.00	0.99	0.99	0.01	0.01	0.99	0.99	0.01	0.01	0.99	0.01	0.99
nul1519	0.99	0.73	0.01	0.99	0.38	0.01	1.00	0.99	0.01	0.01	1.50	0.01	0.01	0.01	0.01	1.50	0.01	0.01	0.01	0.01	0.99	0.99	0.01	0.01	0.99	0.01	0.99
nul1523	0.99	0.58	0.01	0.99	0.30	0.01	1.00	0.99	0.01	0.01	1.50	0.01	0.01	0.01	0.01	1.50	0.01	0.01	0.01	0.01	0.99	0.99	0.01	0.01	0.99	0.01	0.99
sch1409	0.99	0.40	0.99	0.99	0.40	0.99	0.99	0.99	0.01	0.01	1.50	0.01	0.99	0.01	0.01	1.50	0.01	0.99	0.01	0.01	1.70	0.01	0.99	0.01	0.99	0.01	0.99
sch1549	0.99	0.60	0.99	0.99	0.40	0.99	0.99	0.99	0.01	0.01	1.50	0.01	0.99	0.01	0.01	1.50	0.01	0.99	0.01	0.01	1.70	0.01	0.99	0.01	0.99	0.01	0.99
sch1572	0.99	0.58	0.99	0.99	0.37	0.99	0.01	0.99	0.01	0.01	2.00	0.01	0.99	0.01	0.01	1.50	0.01	0.99	0.01	0.01	1.70	0.01	0.99	0.01	0.99	0.01	0.99
chi1485	0.99	0.45	0.01	0.99	0.23	0.99	0.01	0.99	0.01	0.01	2.00	0.01	0.99	0.01	0.01	2.00	0.01	0.99	0.01	0.01	3.00	0.01	0.01	0.01	0.99	0.01	0.99
pot1507	0.99	0.39	0.01	0.01	0.01	0.99	0.01	0.01	0.99	0.01	0.80	0.01	0.01	0.99	0.01	0.70	0.01	0.01	0.99	0.99	2.00	0.01	0.01	0.01	0.99	0.99	0.01