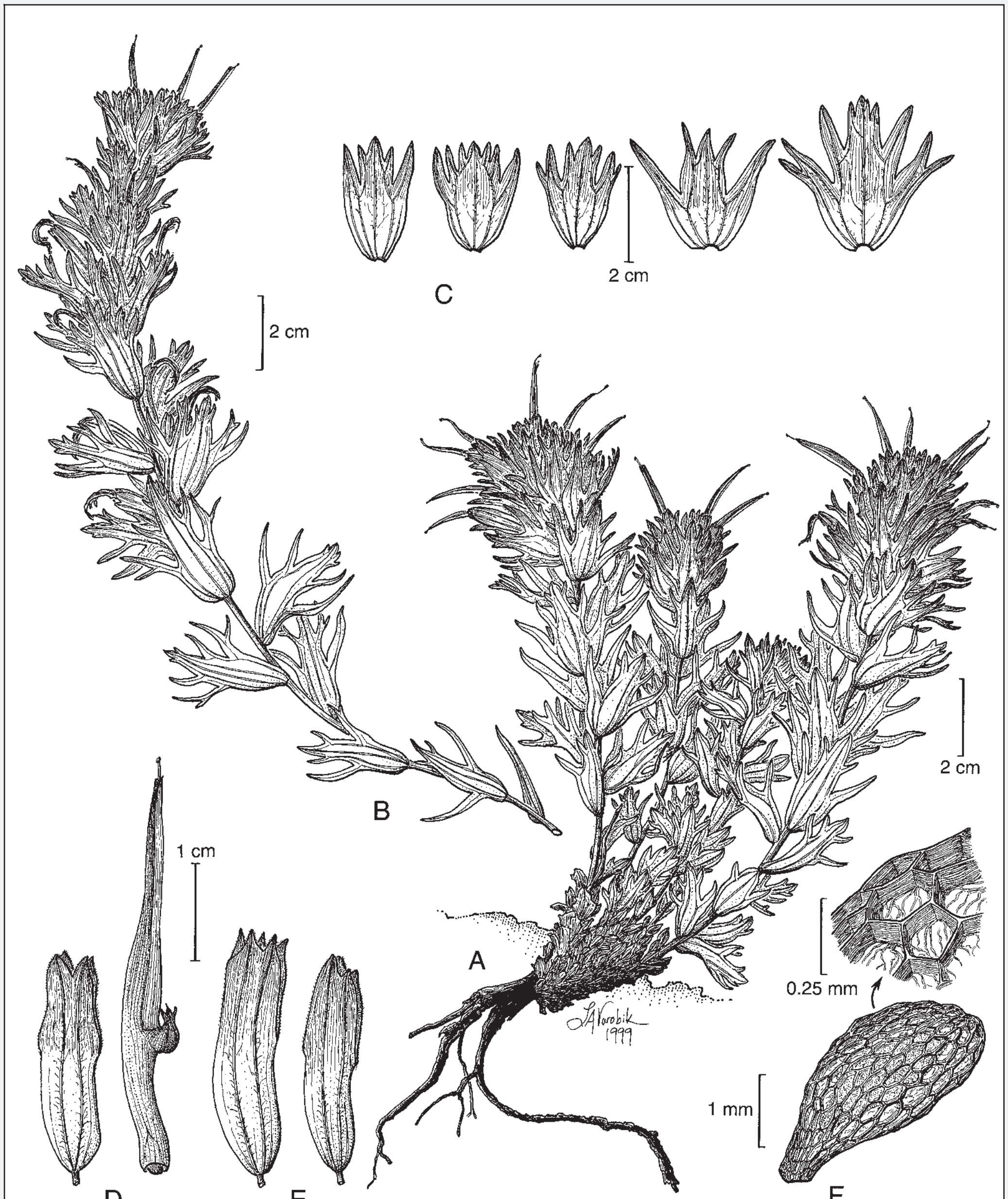
KALMIOPSIS

Journal of the Native Plant Society of Oregon



Castilleja chambersii Egger and Meinke

A, habit; B, flowering stem to show leaf and size; C, bracts; D, calyx with its corolla; E, variability in calyces; F, seed with closeup of wall.

ISSN 1055-419X

Volume 8, 2001

KALMIOPSIS

Journal of the Native Plant Society of Oregon, ©2001

NPSO WEB PAGE

http://www.NPSOregon.org

EDITORIAL

Secrets can be difficult to keep, especially for as long as two years, but we hope that this issue of *Kalmiopsis* surprises the individual that we as NPSO members are all proud to claim as one of our own, Ken Chambers. From front cover through the appendices, every page is dedicated to his honor. Conceived at the time of Ken's seventieth birthday, this Festschrift is the work of many individuals, whom Aaron Liston acknowledges in his introduction. However, Ken's stature as a botanist and as a person is no secret, as noted on the Certificate of Merit presented to him by the Botanical Society of America in August 1990:

> "*Eminent biosystematist, internationally recognized for his studies of various genera of Asteraceae; a pioneer in the development of plant conservation in Oregon; and stimulating teacher who has inspired many students to become botanists.*"

MEMBERSHIP

Membership in the Native Plant Society of Oregon is open to all.

Membership applications, renewals and changes of address (include old address and zip code) should be sent to the NPSO Membership Chair, Jan Dobak, 2584 NW Savier St., Portland, OR 97210-2412

Student $12; Regular $18; Family $24;

Sustaining $50; Patron $100; Life Member $500

Subscription Only (Bulletin and Kalmiopsis) $18

CONTACT INFORMATION

KALMIOPSIS EDITORS: Cindy Roché, 109 Meadow View Dr., Medford, OR 97504, crupinaqueen@home.com

& Linda Ann Vorobik, P.O. Box 866, Lopez Island, WA 98261, vorobik@rockisland.com

BULLETIN EDITOR: Tanya Harvey, 40237 Reuben Leigh Rd., Lowell, OR 97452-9712 bulletin@NPSOregon.org

MEMBERSHIP CHAIR: Jan Dobak, 2584 NW Savier St., Portland, OR 97210-2412, (503) 248-9242

WEBMASTER: Michael McKeag, 7461 SW 184th Pl., Aloha, OR 97007-5740, mmckeag@teleport.com

EMAIL DISCUSSION LIST LOGIN: See NPSO Web Page, select subcribe to list under membership.

WEB PAGE: http://www.NPSOregon.org

COVER ILLUSTRATION

Castilleja chambersii Egger and Meinke, as published in "*Castilleja chambersii* (Scrophulariaceae), a new rare species from the northern Coast Range of Oregon" (Egger, M. and R. J. Meinke. 1999. Brittonia 51(4):445-451). An Indian Paintbrush endemic to the Coast Range of southwestern Clatsop County, Oregon, first recognized as distinct by Ken Chambers, and named for him in 1999 in honor of his 70th birthday.

Kalmiopsis: ISSN 1055-419X. Volume 8, 2001. Published annually. Subscription $18 per year.

Native Plant Society of Oregon

General business address: PO Box 902, Eugene OR 97440

NOTICE TO CONTRIBUTORS

Members of the Native Plant Society of Oregon and others are invited to submit articles, book reviews, artwork, poetry, cartoons, and photographs for publication in KALMIOPSIS. All materials submitted should pertain to Oregon's vegetation and flora. Acceptance will be based on suitability (articles dealing with formal nomenclatural proposals or of a highly technical nature are not acceptable).

Contributors of articles should submit one hard copy of a double-spaced manuscript accompanied by an electronic copy of the file (PC or MAC; Word, Word-Perfect, or a Text or Rich Text Format File; indicate name of Program and Version in the accompanying cover letter). Computer facilities are available for use at libraries and printing or word-processing businesses.

Contributions without accompanying manuscripts, such as art, cartoons, or photos, also are welcomed.

Send all submissions to KALMIOPSIS EDITORS, or e-mail KALMIOPSIS EDITORS to request an electronic submission. (Specific instructions for submission of photographs, figures, and tables will be sent to contributor upon request or after article has been accepted for publication.)

Please feel free to contact KALMIOPSIS EDITORS for further information, or to inquire if an article is suitable for publication in this journal.

ACKNOWLEDGEMENTS

Kalmiopsis Logo: Linda Ann Vorobik (VorobikBotanicalArt.com)
Pagesetting: Cindy Roché and Linda Ann Vorobik
Art work: © Linda Ann Vorobik
Printing: Mustard Press, (MustardPress.com)

TABLE OF CONTENTS

PURPOSE

~ Native Plant Society of Oregon ~

Dedicated to the enjoyment, conservation, and study of Oregon's native vegetation.

Kalmiopsis
Native Plant Society of Oregon
Jan Dobak, Membership Chair
2584 NW Savier Street
Portland, OR 97210-2412

NONPROFIT ORG
US POSTAGE
PAID
MEDFORD OR
Permit No.113

A Festschrift Honoring Kenton L. Chambers

Aaron Liston
Herbarium Director, Oregon State University, Corvallis, OR 97331

Festschrift is the German word for "celebratory writing," a unique publication devoted to the research and influences of an exceptional scholar. In this issue of *Kalmiopsis*, we celebrate the career and accomplishments of Kenton Lee Chambers on the occasion of his 70th birthday on September 27, 1999. Ken has made important contributions to plant systematics through his monographic and biosystematic studies of *Microseris* (Asteraceae) and related genera. He published the new genus, *Stebbinsoseris*, in honor of G. Ledyard Stebbins. A dedicated and inspiring instructor, he taught plant systematics, plant evolution, and agrostology to hundreds of students at Oregon State University, and served as major professor for 16 PhD students and 16 MSc students in plant systematics. In 1989, Ken received the OSU Alumni Distinguished Professor Award. Ken is a pre-eminent authority on the flora of Oregon, having worked in the field since his arrival at OSU in 1961. Since his retirement from OSU in 1990, he has continued his herbarium and field studies and has been a major contributor to the Oregon Flora Project. He has collected over 6,250 specimens during his botanical career, and he still is collecting! Ken was a co-author with Jean Siddall and Dave Wagner of the first enumeration of rare, threatened and endangered vascular plants in Oregon, and his efforts towards plant conservation in Oregon continue to this day. In recognition of his botanical accomplishments and his contributions to the passage of the Oregon Endangered Species Act, the Native Plant Society of Oregon in 1999 named him a Fellow of the Society, the NPSO's highest award.

The lead article of this festschrift is a biography written by the person who knows Ken best, Henny Chambers, his wife of 43 years. Her numerous insights into Ken's personal and professional life will provide the reader with another dimension to the life of this most talented man. This is followed by a description of Ken's key role in the preservation of Oregon's native plants, written by Rhoda Love, Secretary of the Native Plant Society of Oregon. In her letter nominating Ken for "Fellow of the NPSO," Rhoda, upon listing his accomplishments and contributions for this award, concludes by writing, " ...and, most especially, an accessible person who has never been too busy to promptly and fully answer the countless taxonomic questions that constantly come his way from all of us." The next two articles were written by three of Ken's graduate students and reflect his biosystematic and floristic interests. Richard Halse and Judith Glad give a floristic account of Walker Flat, an upland meadow-wetland complex in the Coast Range of Yamhill County, Oregon. Wayland Ezell presents the taxonomic conclusions from his genetic and ecological studies of two central Oregon *Mimulus* species. The final article, by Konrad Bachmann, a longtime colleague, describes Ken's contributions to the systematics of the genus *Microseris* (Asteraceae). In reference to Ken's taxonomic abilities, Dr. Bachmann writes, "Spotting the right characters and interpreting them properly ... has been the decisive ability of great taxonomists. Kenton Chambers has this gift to perfection." *Microseris* was the subject of Ken's PhD thesis, and its taxonomy and evolution remain one of his central interests. Together, these five articles celebrate the breadth and influence of Ken's botanical career.

I wish to acknowledge the role of Nancy Fredricks in the initial development and organization of this festschrift. Nancy conceived of the idea of celebrating Ken's 70th birthday with a book of writings dedicated to him. She initially contacted prospective authors and collected the manuscripts. The articles were then edited and proofread by Wayland Ezell. I am extremely grateful to him for his time and dedication to the project.

ODE TO A TAXONOMIST

Botany, chess and music:
Baritone horn, piano and
Gilbert & Sullivan in song.
An eclectic fellow, he's
A man for all seasons.
Even limericks flow
From the pen
Of this talented chap.
Eagle Scout to professor,
Stanford to Yale,
And then to Oregon State.
His career is replete with honors:
Distinguished Professor, botanical fellow,
With publications galore.
Rare and endangered plants survive
Through his tireless efforts, and
With plant press in hand,
He records another find on serpentine.
Taxonomist, collector and curator.
A Mircoseris by any other name
Will not escape his keen eye.
In the world of taxonomy,
This trinomial says it best:
Kenton Lee Chambers.

Wayland L. Ezell
September 2000

Ken Chambers, Oregon Botanist

Henrietta Laing Chambers
4761 Hollyhock Circle, Corvallis, OR 97333

KEY WORDS: *Kenton L. Chambers, biography, botanist, Oregon plant conservation*

*Abstract***.** The author shares her perspective in this personal and professional biography of Kenton L. Chambers, long-time taxonomist at Oregon State. His plant specialties are: Asteraceae, Tribe Cichorieae, and the genera *Microseris*, *Agoseris,* and their relatives, as well as *Claytonia* (Portulacaceae). Chambers taught Agrostology and became expert in the grasses, although he did not publish in that field. He has had a great influence on the conservation of rare and endangered plants in Oregon and served as teacher or major professor for many plant taxonomists in Oregon and the nation. Appendix I lists Chambers's graduate students and their thesis titles and Appendix II his publications.

Kenton L. Chambers was born in Los Angeles, California, on September 27, 1929. His parents, Edna (Miller) and Maynard Macy Chambers, had met at the Osteopathic College there and married shortly after graduation. His maternal grandparents, Josephine (Schwab) and Calvin Miller, had a strong influence on his life. They had moved west from Clay County, Nebraska, where they had been farmers, to Atascadero, California, in San Luis Obispo County, when Ken's mother was nine years old. The parcels of land in Atascadero that were sold to farmers from all over the country for growing fruit (mainly peaches) were too small to support a family, and money was always in short supply. The Miller family remained in Atascadero until it was time for Ken's mother to go to college. They moved to Los Angeles when she chose to attend the University of Southern California. When we attended a Schwab family reunion in Nebraska in the spring of 1998, Ken had a chance to stand in a fallow field that his grandfather Cal Miller had farmed as a young man. He could understand why a hard-working young farmer would choose to move west. Ken brought back some soil to show his children his prairie roots.

Ken's only sibling, his brother Derrell Lynn Chambers, was born in 1934. He was five years behind Ken in school, and it wasn't until he came to Corvallis to do graduate work at Oregon State (1961-1965) that the brothers had a chance to know each other as adults. They have many traits in common and enjoy each others' company. Derrell also is a scientist, an entomologist, who received his PhD at Oregon State University in 1965 and spent most of his career with the United States Department of Agriculture. His research on fruit flies took him to labs in Maryland, California, Hawaii, Florida, Mexico, and Guatemala. The last 10 years of his career were with the US State Department in Guatemala City.

Ken spent his early childhood in Pasadena. His parents divorced when he was ten years old, and his mother returned to college in Whittier to obtain a degree in counseling. Some of the most vivid memories (and nightmares) Ken has of his childhood are riding the city bus from Whittier to Pasadena, by himself, for his weekly piano lesson. He still remembers many of the techniques and admonitions of his teacher, Ora Leola Caldwell. He became proficient enough to give a solo recital when he was ten years old and again when he was twelve. He also sang in a boys choir that was sponsored by a local funeral home in Whittier. He took up the baritone horn in junior high and then switched to the trombone in high school. When his mother moved to Corvallis in 1970 to be nearer to Ken and his family, she brought all of his old piano music, and he could play many of these old pieces after a quick glance at the music. His mother was a good pianist too, and they enjoyed playing duets. His participation in music, other than just playing the piano for relaxation and the enjoyment of his family, took a back seat to his botany career until his retirement.

Ken's mother finished her studies at Whittier College at about the time World War II began. They moved to Laguna Beach for a short time, and Ken remembers the wonderful times playing in the tide pools, building forts and digging caves in the sandy bluffs above the beach with his brother. For a school project, he assembled a picture scrapbook of all the allied and enemy warplanes and learned to identify them from their silhouettes. As the war continued, there was a shortage of science teachers, and in 1942, "Doc" Chambers, as his mom was called, accepted a position at Paso Robles High School, a few miles north of Atascadero, where she had lived as a child. She taught biology, chemistry and physics, and she was Ken's teacher for all his high school science courses. This was a difficult situation for a young man who was new in town and just trying to fit it and be one of the guys. Paso Robles was a small farming town which happened to have a large Army base (Camp Roberts) nearby, and his Boy Scout troop had leaders from the base. Ken eventually attained the rank of Eagle Scout. He appreciated his other high school classes, particularly typing (2 years!) and English, both of which had extremely good teachers. He played junior varsity basketball, played trombone in a swing band called "The Ramblers", and played in the marching band. He played trombone in the marching band in college and even played during his first year of graduate study at Stanford.

Ken received a four-year scholarship to attend Whittier College and in his class there were several students he had known during his early school years in Whittier. In Ken's freshman year at Whittier, in the fall of 1946, Henry J. "Harry" Thompson was in the same General Zoology class. Harry was a senior, just back from the war in the Pacific, and he remembers getting beat on the exams by a "smart-ass" freshman named Ken Chambers. Harry went to Stanford the next year, did a masters degree in Botany and then came back to teach at Whittier in 1948 (for Lois James, Whittier College biologist, who went on sabbatical leave to Stanford to complete her PhD). In the fall of 1948, Ken took Comparative Anatomy from Harry, and they studied the usual animals in lab: the shark, *Necturus*, a salamander and the cat. Ken made 100 percent on all the lab practical exams. Harry then made them harder, which made all of the other students get lower grades, but Ken still got 100 percent. Harry went home for the holidays and salvaged some of the bones from his mother's turkey soup and put a few of them on the final lab practical. As Harry said, "I finally found his weakness. His knowledge of the bird pectoral girdle was less than perfect."

Another memorable Harry Thompson story from Whittier days tells of Ken taking field botany from him in the spring of 1949. "Ken specialized in Compositae, as we called them in those days, because everyone else in the course, including the instructor, knew very little about them. I think he was getting even for the turkey bones. Ken made excellent plant collections in the class, mounted his specimens on 8 1/2 x 11 inch botany drawing paper and arranged them, using the Engler and Prantl System, in an orange crate. He brought this collection to Stanford where he took lots of kidding about his Orange Crate Herbarium."

While at Whittier, Ken also became an accomplished chess player. He would buy the *Los Angeles Times* on Sundays and go back to his room and try to solve the chess problem that was a weekly feature of the column by Herman Steiner. Several times his solutions were winners and featured the following week. Occasionally, he was able to go to the Los Angeles Chess Club to play. He played tournament chess in Oregon for a short time in the early 1980s and won a trophy cup for the Top Senior in the 1981 Oregon City Open tournament. He was ranked as a Class A player (just below Master). He found tournament play a bit too stressful, but he still enjoys playing games out of books and magazines, on his computer, and with his grandchildren. He has assembled quite a nice chess library.

After graduating from Whittier College in 1950, Ken went to Stanford, following in the footsteps of his former teachers, Harry Thompson and Lois James. There was an active group in vascular plant systematics which included Dr. Ira Wiggins, Roxie Ferris, Dr. Richard Holm, Harry Thompson, John Thomas, George Gillette, Vic Stombler, George Ward and Robert Vickery. Dr. Edgar Anderson from the Missouri Botanical Garden was a visiting professor one spring and, from the photographs I have seen, he provided much color in his field trip outfit: a Nehru hat and Mexican serape. There were memorable field trips to the desert and Sierra Nevada with graduate students and professors. Ken's PhD thesis, *A Biosystematic Study of the Annual Species of Microseris*, was completed under the direction of Dr. Wiggins. Ken was a teaching assistant in General Biology from 1950-1953 and was supported by a National Science Foundation Pre-doctoral Fellowship in 1953-54.

It was through Ken's graduate work with Dr. Wiggins that he had the opportunity to work at the Office of Naval Research-sponsored Arctic Research Laboratory in Point Barrow, Alaska. He was there from June to September in 1951, collecting vouchers and buds for cytological studies of flowering plants growing in permafrost communities. Dr. William C. Steere was one of the Stanford botanists on that trip; and Ken was impressed with his enthusiasm for bryophytes and other things botanical, his sense of humor and his scientific skills. Ken is an excellent correspondent, and he wrote very detailed letters to his mother describing the scenery, Eskimos, particularly the children, and the field and laboratory work he was doing. She decided to share these wonderful letters with the local Atascadero newspaper. Needless to say, he was not very happy!

Ken Chambers, Eagle Scout, 1946.

When he completed his thesis in June of 1955, Ken took a five-week field trip to Baja California with fellow Stanford graduate students, botanist Vic Stombler and entomologist John Figg-Hoblyn. He learned many desert plants and made herbarium and bud collections. Some of the memorable moments were collecting insects at night in the headlights of the Jeep and sleeping under the stars in the desert. His work resulted in a paper, "A Collection of Plants from the Eastern Flank of the Sierra San Pedro Martir, Baja California," published in the *Contributions of the Dudley Herbarium* in 1955 [see Appendix II]. He then embarked upon an NSF Post-doctoral Fellowship under Dr. Harlan Lewis at UCLA, counting chromosomes of Asteraceae and other families.

The fall of 1956 brought a real change in scenery for the native Californian. Ken found himself in New Haven, Connecticut, in the Ivy League, first as Instructor and then as Assistant Professor in the Department of Botany at Yale University. It took time to get used to the cold, snowy winters, but when spring arrived, he enjoyed getting out in the field. He rose to the challenge of learning the eastern flora and began to explore the research possibilities of some eastern chicory tribe genera such as *Prenanthes* (RATTLESNAKEROOT)

Ken Chambers in Baja California, 1955.

and *Krigia* (DWARFDANDELION). He had a whole greenhouse room of *Microseris* growing, flowering, and fruiting so he could continue his thesis research. He taught in the General Biology course and developed a graduate course entitled "Variation and Evolution in Natural Populations". He made some life-long friends among his colleagues: Oswald Tippo (department chair and plant anatomist), Ted Delevoryas, (paleobotanist), and William L. Stern (wood anatomist in the Yale School of Forestry).

It was through his association with Bill Stern that he made three collecting trips to the tropics: to Panama in the summers of 1957 and 1959, and to the Florida Keys in March of 1958. The first Panama trip was under the sponsorship of the Biology Branch, Office of Naval Research. The Panamanians believed that their local trees had natural resistance to marine-boring organisms (teredos or shipworms). Stern and Chambers proposed to help locate, collect, and identify as many Panamanian hardwoods as they could. The local hardwoods would then be tested at the Canal Zone Corrosion Laboratory, US Naval Research Laboratory. This would allow the Panama Canal Company to use a local material instead of creosote-soaked Douglas-fir posts, pilings, and lumber that came from the United States. Shortly before they left Yale, they received a list of potentially resistant trees, but it was a list of common names. Fortunately, Dr. Stern's assistant at Yale, Dr. George K. Brizicky, had the opportunity to search out the scientific names. They did make arrangements for collecting most of the timbers on the list. The collecting areas were Canal Zone; Volcán Region, Chiriquí Province; vicinity of Almirante, Bocas del Toro Province; Puerto Armuelles, Comarca del Barú; and Bahia de Piñas, Darién Province. The scientific contributions of this trip were the collections that Dr. Stern and Ken made for the Wood Collection at Yale (which is now part of the Samuel J. Record Memorial Collections of the US Forest Products Laboratory at Madison, Wisconsin) and a publication in *Tropical Woods* entitled "A Collection of Woody Plants from Panama." The woods were tested in the canal and at both the Atlantic and Pacific entrances. The results of the testing for resistance to marine borers were reported in internal Office of Naval Research documents. One of Ken's special assignments on this trip was taking 8 millimeter movies on a small Bell & Howell camera. Although tropical forests are very dark, he got some good footage of collecting, the removal of trees to the testing areas, and of ships traversing the canal.

Six months after the collecting trip to Panama, Bill Stern fell ill with malaria, and it remains a mystery why Ken did not. They both had been taking quinine while they were in Panama, but their doctor had failed to tell them that they should continue the drug after they returned home. However, by March, 1958, Bill had recuperated and was ready for a trip to the Florida Keys with Ken, where they collected wood samples with herbarium vouchers for Yale. As Bill recalls, the Keys were still fairly heavily vegetated and undeveloped, compared to the houses, condominiums, fishing camps, and resorts that you find there today. He also remembers that Ken was quite good at composing limericks which were recorded in their field notebooks. Bill had recently referred to the books and sent copies of the limericks to me. Some of them are botanical in subject, but that is not reason enough to include them in this biography! Ken solved a taxonomic problem in the Sapotaceae family when he was able to determine that an unusual tree was quite different from nearby trees of the same species, and that it was a triploid of low fertility which probably had arisen spontaneously. (See: "On the Origin of an Unusual *Dipholis* from the Florida Keys", Chambers 1960 in Appendix II).

The 1959 Panama trip was funded by the Office of Naval Research, CIBA Pharmaceutical Company, United Fruit Company and indirectly by the National Science Foundation, through their grant to the Missouri Botanical Garden for the Flora of Panama project. The latter was the largest investor, and they wanted well-documented specimens and one of their adjunct botanists, Dr. John Dwyer from St. Louis University, to be included in the trip. John Ebinger, a graduate student in botany at Yale working with Dr. John R. Reeder, also became part of the group. Bill Stern provided me with a report written by John Ebinger that was taken from a diary or journal that he kept. It was John's first trip to the tropics, and it provided many insights. The difficulty of transportation and collecting in the tropics is not to be minimized. The team decided they were most efficient working in pairs, doing their collecting in the mornings and pressing in the afternoons. They were making five sheets of each collection, and the task of pressing them was arduous. Many tropical fruits are large and woody and do not lend themselves to pressing. Drying the specimens was also difficult, because they often stayed in buildings with leaky roofs, and tropical rainstorms occurred almost every day.

While at Yale, Ken also had a very memorable spring field trip with Reed Rollins to Texas collecting *Lesquerella* (Brassicaceae: BLADDERPOD). He was always eager to be in the field in a new part of the country and to collect and key new plants. In addition, he collected some excellent teaching material that showed the differences in fruit shapes between some of the taxa, as well as some variation between populations of the same species of *Lesquerella*.

In the fall of 1957, I became acquainted with Ken when I enrolled as a graduate student in the Botany Department at Yale. He was one of the faculty coordinators of the teaching assistants in the General Biology course. I had grown up in Westchester County, New York, but it was as an undergraduate at Maryville College (Tennessee) and a graduate student at the University of North Carolina (UNC) at Chapel Hill that I became interested in botany. I had just finished my Master's degree at UNC, and for my thesis I had completed a flora of Harnett County, North Carolina.

On our first date, we attended a football game at the Yale Bowl on a cold and beautiful fall afternoon. We also liked to go for drives in the countryside, looking for places to hike and to see the native flora. It was on field trips to the North Haven sand plains, West Rock, the Yale Preserve, Yale Forest and Lighthouse Point, along with the football games and Botany Department gatherings, that we realized how much we enjoyed each other's company.

Our friendship blossomed into a romance, and in June, 1958, we were married in New Rochelle, New York, my hometown. We spent part of our honeymoon at a small resort in Rindge, New Hampshire, hiked up Mount Monadnock and also drove the toll road up Mount Washington. In the fall of 1995, we retraced our journey. The small resort hotel, which was really a large farmhouse, and the recreation barn had been renovated and were now at the center of the campus of Franklin Pierce College, a small liberal arts college that had been founded in 1962.

Right after our honeymoon, we began collecting *Pycnanthemum* (Lamiaceae: MOUNTAINMINT) for my thesis research. This was a genus I had become familiar with in North Carolina. I planned to use a cytological approach, counting chromosomes and analyzing artificial and natural hybrids. I chose to work with Ken as my major professor.

Ken continued his *Microseris* research and gave papers at the American Society of Plant Taxonomy meetings in 1956, 1957, and 1959. In both 1957 and 1959 he received the George R. Cooley Award, with a cash prize of $100, for the best paper presented.

In 1960, Ken was offered a position of Associate Professor in the Department of Botany and Plant Pathology at Oregon State College (changed to Oregon State University in 1961). He visited the campus and met the chairman, Dr. Roy A. Young, and other members of the department in the spring. There was to be a merger of the Botany and Zoology departments at Yale within the next year, and although he was encouraged to stay at Yale, Oregon State looked like a good opportunity for a plant systematist.

Our daughter, Elaine, was born in New Haven in May, three months before we moved to Corvallis. Needless to say, a cross-country automobile trip with an infant and pulling a U-Haul trailer had both good and bad moments. The next-to-last day of the trip was a memorable one. Driving our 1955 two-door Chevrolet, we crossed almost the entire width of Oregon, from Ontario to Albany. When traveling with a baby it is hard to get an early start, and we left Ontario after 9:00 a.m. It is a 157-mile "leg" to Burns through the sagebrush-juniper desert, a new experience for me, although Ken was familiar with the deserts of Nevada and California. It was time for lunch in Burns and then 133 miles to Bend, time for a snack and rest stop in mid-afternoon. It is 121 miles from Bend to Albany. I was the navigator, but I was unfamiliar with mountains, so it looked like any other 121 miles of highway. We crossed the Santiam Pass (4,817 feet) and Tombstone Pass (4,236 feet) and started down the west slope of the Cascade Mountains. We passed a small cafe at Upper Soda, but decided it was too early for dinner, and it was just a "little" farther to Sweet Home. Well, when an infant gets ready for food and activity, and none is in sight, it can be a bit harrying. Ken didn't tell me until later that the brakes were becoming less effective during the descent. I recall it was almost dark when we arrived in Sweet Home, and the restaurant sign that attracted our attention was in a bowling alley near the west end of town. The noisy meal was one we chose to forget quickly.

At Oregon State, Ken succeeded Dr. Albert Steward who had died in 1959. Dr. Helen Gilkey (with Emeritus status having retired in 1951) still was coming to the Herbarium frequently, and Ken enjoyed their association. In the year between Dr. Steward's death and Ken's coming to OSU, LaRea Dennis was acting curator of the Herbarium. She remained as assistant curator for his entire tenure at OSU, and their skills and interests complemented each other.

We liked Corvallis immediately. We rented a spacious house for our first year. In June of 1961, we bought a house about ten blocks from the campus, and in September, our son Dave was born. The house was well-cared for, but the garden was overgrown, and the lawn had been neglected. So Ken got busy renovating the lawn and restoring the garden. Our 1964 photos that show a really nice perennial garden with early primroses, daffodils, and narcissus complemented by a flowering apple, crabapple, and plums. Later in the season there were iris, lupine, columbine, calla lilies, and fuchsias.

One of the courses that Ken developed at Oregon State was Agrostology, a service course for agriculture and range science majors, as well as a course for botany majors. He continued to teach this course until 1994, four years after his retirement. I think what he liked best about Agrostology was that it allowed him to become expert on that large, difficult grass family! His teaching load was much greater than it had been at Yale. His plant evolution class began as a three-term sequence, which he eventually changed to a five-credit winter-term class. He also taught in the Core Biology program for many years. His spring term plant families course, Botany 321, required fresh plants each Monday for a review with the teaching assistants and then later in the week for students in the lab sections. The enrollment of that course grew steadily through the years, and this meant a lot of plants! I often accompanied him on Sundays, driving around Benton County or to the coast, to the localities he knew certain plants could be found. He also offered Saturday field trips for students to the Columbia River Gorge, Central Oregon and the Cascades, and an overnight trip to southern Oregon. Now that we are retired, we look back on the memories fondly, but at the same time we are glad that someone else is teaching the class and collecting the plants.

Ken was the local representative of the American Society of Plant Taxonomists when they met with the American Institute of Biological Sciences (AIBS) in Corvallis in August, 1962. He organized two symposia, led a two-day pre-meeting field trip and made arrangements for the banquet. He was a participant in one of the symposia: "American Amphitropical Plant Distribution," where he shared the podium with Lincoln Constance, Larry Heckard, Robert Ornduff, and Peter Raven. His paper entitled "Amphitropical Species Pairs in *Microseris* and *Agoseris* (Compositae: Chicorieae)" was published with the others in the *Quarterly Review of Biology* in

1963. The fun part of the AIBS meetings was that it was a chance for us to host an open house for many of our old friends from Yale and graduate student days.

Ken always had a greenhouse full of *Microseris* and *Krigia* for his continuing population studies, which included making artificial hybrids. He also built up a large collection of achenes (fruits), not knowing that one day he would have a *Microseris* colleague in Europe. Often he would continue projects begun by graduate students. He served as major professor for 16 PhD students and 16 MS students. The genera studied in these projects show great diversity: *Achillea*, *Agrostis*, *Artemisia*, *Aster*, *Crepis*, and *Microseris* (Asteraceae); *Cryptogramma* and *Hackelia* (Boraginaceae); *Arabidopsis* (Brassicaceae); *Arctostaphylos* (Ericaceae); *Astragalus, Lathyrus,* and *Sophora* (Fabaceae); *Phacelia* (Hydrophyllaceae); *Pycnanthemum* (Lamiaceae); *Collomia* (Polemoniaceae); *Claytonia* (Portulacaeae); *Mentzelia* (Loasaceae); *Mimulus* (Scrophulariaceae); *Juncus* (Juncaceae); *Calochortus* and *Trillium* (Liliaceae); *Triticum* (Poaceae). (A list of Ken's graduate students and their thesis titles is included in Appendix 1.)

Ken Chambers in OSU Herbarium, 1988.

Ken returned to the tropics in 1966 when he went to Dominica as part of a flora project under the direction of the Smithsonian Institution. He spent three months at Clark Hall, a coffee plantation/guest house on the Layou River, the headquarters for the visiting scientists. He was able to take day trips to all areas of the island and return in the evening to press his collections. He was most impressed with the pygmy forests on the high peaks: Morne Trois Pitons and Morne Diablotin. He was there for Carnival and had a chance to see the wonderful steel bands parade through the streets of the capitol, Roseau. In 1994, Ken and I took a Caribbean Cruise that included a stop in Dominica. We had a bus trip from Cabrits to Roseau, with a stop for lunch at the Layou River Hotel. Ken thought the area looked very familiar, and he walked out to the road and saw the much-changed Clark Hall just a short distance away. It looked a bit overgrown and had gone back to being just a plantation. He heard from one of the ladies serving luncheon at the Layou River Hotel that it had been severely damaged in a hurricane.

For several years in the mid-1960s Ken had been on the Grants Panel in Systematic Biology for the National Science Foundation (NSF). In the fall of 1967, he took a leave of absence from OSU to be Program Director for that group. Washington, DC, was an exciting place to be that year; we did a lot of sight-seeing, and left with many memories. We lived in Kensington, Maryland, in the home of Dr. Walter Hodge, an NSF program director who had taken an assignment in Japan. We particularly appreciated the beautiful garden at his home, featuring rhododendrons, azaleas, hostas, redbud, and dogwood. We had several collecting trips to the mountains in Virginia and North Carolina, allowing us to bring many collections of *Krigia* and *Pycnanthemum* back to Corvallis. Unfortunately, 1968 was a year for unrest in the District, brought on by the assassinations of Martin Luther King and Robert Kennedy.

Before Ken agreed to go to Washington in the fall of 1967, he was named chairman of the Biology Colloquium Committee at OSU. The Biology Colloquium is an annual event with broad support from the science, agriculture and forestry schools. The topic was "Biochemical Coevolution," and Ken and the Committee lined up the speakers: Paul Ehrlich, Cornelius Mueller, Stephen Karakashian, Peter Atsatt, Lincoln Brower, Calaway Dodson, and Robert Hull. He came west for the event in the spring of 1968 and edited the volume which was published by the OSU Press in 1970.

Ken has led some interesting field trips for visitors to the Pacific Northwest. One was a pre-Congress field trip before the 1969 International Botanical Congress in Seattle. One of the participants on that trip was a graduate student in taxonomy, Melinda Denton from the University of Michigan. Of course, she eventually became a northwest colleague when she became a faculty member at the University of Washington. In September of 1979, Ken hosted three botanists from the Soviet Union on an extended trip throughout Oregon and northern California. The trip was under the sponsorship of the USA/USSR Botanical Exchange Program and coordinated by Thomas Elias of the Cary Arboretum of the New York Botanical Garden. The total trip was to be over one month and include Washington, Oregon and California to allow the visitors to see many different plant communities and to collect seeds of woody plants. Ken was asked to help with the Oregon and California part of the trip. The Soviet botanists were Dr. Valeri Nekrasov, Main Botanical Garden, Moscow; Dr. Ivan Krasnoborov, Siberian Central Botanical Garden, Novosibirsk; and Dr. Isa Baitulin, Director, Botanical Garden, Alma-Ata. They went to the coast, as far south as the Oregon Dunes, to Mount Hood and the Columbia River Gorge, Central Oregon and Crater Lake, Siskiyou Mountains, and into California to the Redwood National Park. Ken received holiday greetings and corresponded with these botanists for several years after the trip, and they were pleased that many of the seeds they collected had germinated.

In the mid-1970s, Ken became involved in the Oregon Interagency Task Force on rare and endangered species made up of botanists (government, university, amateur) from all over the state. They reviewed the Oregon species in the National List compiled by the US Fish and Wildlife Service. He collaborated with Jean Siddall and Dave Wagner to author "Rare, Threatened and Endangered Vascular Plants in Oregon—An Interim Report" that was published by the Oregon Land Board in 1979. It includes data on distribution, abundance, habitat and ecological requirements of almost 400 native species. Later, in April, 1991, Ken was recognized with a plaque for: "over a decade of high standards, integrity and support for the Region 6 Sensitive Plant Program."

In 1974, the Chambers family embarked on a project that has given us much pride and pleasure for the last 25 years. We purchased a log cabin kit and built a vacation cabin in the Camp Sherman area, not far from the headwaters of the Metolius River. From June through August, we drove over the mountains on Friday mornings, set up camp at the closest campground to the Camp Sherman Store and then went to work assembling our giant "Lincoln Log" house. Ken was a demanding taskmaster, and we learned quickly that if he wanted a tool or piece of lumber, we jumped to get it and put it in his hands. We had a few friends and neighbors from Corvallis who helped when the roof beams needed to be lifted and put in place. Ken completed the roof decking and cedar shakes by himself because summer vacation had ended, and the children had to return to school. In late 1997 we had a deck built to provide better outdoor living there and to commemorate our 40th wedding anniversary. Our children, then in their late 30s, were there with their children, family, and friends for the celebration.

In the late 1970s Ken began his collaboration with Dr. Konrad Bachmann, a Biology faculty member from the University of Heidelberg. This has led to a number of co-authored publications (Appendix 2). Konrad was a geneticist who used frogs as his experimental organism, but who became discouraged at the difficulty of keeping his genetic stocks alive and healthy in the lab. He came across Ken's thesis (published in the *Contributions of the Dudley Herbarium* in 1955) and thought *Microseris* would be a good genus for researching the genetics of the Compositae head. (He specifically studied pappus number and type, number of flowers per head, flowering time and other observable differences in plants grown in a uniform environment.) Konrad came to Oregon in 1978, and Ken took him on a field trip to "*Microseris* Country." He also showed him how well they grow under greenhouse conditions and gave him lots of fruits to start his studies. In 1983, we spent the spring term in Heidelberg, Germany, where Konrad had his lab in the Biology for Medicine Department. Konrad had his spring "crop" of over 1,000 *Microseris* plants in individual pots in two large greenhouse rooms. Ken made over 80 cross-pollinations, helped "score" the plants as they matured in the greenhouse, and studied chromosome pairing at meiosis in many hybrids. I too worked in Konrad's lab that spring and "scored" 10,000 achenes from heads that were collected the previous year. Our collaboration provided Dr. Bachmann with hybrid achenes for many years work (see Bachmann article in this issue).

It was a working spring, but Germany was new to us, and Konrad and his wife Hannah made sure that we had an outing each weekend (after watering in the greenhouses!). Some of the wonderful one-day trips we had were to Stuttgart, Bad Wimpfen, Worms, Weinheim, Darmstadt, Schwetzingen, Rothenburg, and the Black Forest. The trips were a mixture of cathedrals, castles, Roman ruins, bridges, towers and summer palaces, as well as animal parks, managed forests, arboreta and botanical gardens. The Neckar River, which flows through Heidelberg, flooded in April, and it was the wettest May in 30 years and the coldest May in 100 years, and it flooded again. We walked more, rain or shine, than we had in Corvallis in many years. Before returning home we spent two weeks in England, including a day at Kew Gardens, a place of botanical fame. We both had looked forward to the visit and had a wonderful day.

Ken became so interested in some of the genera that many of his students worked on that he often collaborated with them on later projects. (I was the only graduate student he had at Yale, and he collaborated with me in my post-thesis research on artificial and natural hybrids in *Pycnanthemum*.) He collaborated with John M. Miller and Charles Fellows on *Claytonia*, and with Mickey Dean and Gerry Allen on the *Aster foliaceous* complex. For the past few years he has been collecting and growing many collections of an herbaceous, perennial *Artemisia*, a continuation of thesis work by Jim Estes. In the course of his collecting, he has come across new species, which he usually grows in the greenhouse or in pots at our home before he publishes the descriptions. Currently, he is growing a potential new species of *Dodecatheon* collected from Saddle Mountain and the Trask River in Clatsop County for flowering and fruiting study material.

Many manuals and floras have been published with Ken's treatments of the Chicory genera: *Nothocalais* and *Microseris* in *Illustrated Flora of the Pacific States* (1960) and *Agoseris*, *Microseris*, *Nothocalais*, *Phalacroseris*, *Stebbinsoseris* and *Uropappus* in the 1993 edition of *The Jepson Manual*: *Higher Plants of California*. He also did the treatments for *Claytonia* and *Montia* in *The Jepson Manual*. He did the treatment of *Thuja* for volume 3 of the *Flora of North America* (1993), and he currently is a regional editor for *FNA*. His professional publication record includes over 128 scientific articles and abstracts, taxonomic treatments, book reviews, and articles for amateur botanists (see Appendix II).

Ken has been a member of many professional societies since his graduate student days: American Society of Plant Taxonomists (ASPT), American Association for the Advancement of Science (AAAS), Botanical Society of America (BSA), American Institute of Biological Sciences (AIBS), California Botanical Society (CBS), and International Association of Plant Taxonomy. He served in leadership capacity for some of these organizations throughout his career: ASPT Council member (1972-1978), Membership Committee Chairman (1975-76), Committee on Environment and Public Policy (1976-1980), and President (1979); AAAS Pacific Division Executive Committee (1984-1990), member Local Organizing Committee for Meetings (June, 1988), Fellow of AAAS (1989); BSA Systematic Section Chairman (1965-1967), Pacific Section Chairman (1970 and 1978), Elections Committee Chairman (1973), and Career Merit Award (1990); AIBS local representative for the Corvallis meetings (1962 and 1975), member of editorial board of *BioScience* (1971-1976); and CBS member of editorial board of *Madroño* (1968-1974).

In 1988, Ken was again to be local representative for meetings at OSU. This time it was the AAAS, Pacific Division, and he organized and chaired a symposium entitled "The Future of Endangered Plant Species Studies in the Pacific Northwest." He also organized and led a field trip to the Columbia River Gorge, which included a two-hour ride on the sternwheeler "Columbia Gorge" from Cascade Locks.

In 1989, the year before Ken retired from Oregon State University, he received the OSU Alumni Distinguished Professor Award. He was deeply moved by this honor. In August, 1990, he received a Certificate of Merit from the Botanical Society of America with the citation, "Eminent biosystematist, internationally recognized for his studies of various genera of Asteraceae; a pioneer in the development of plant conservation in Oregon; and stimulating teacher who has inspired many students to become botanists."

In his retirement Ken has continued his favorite parts of his teaching and research career. I suppose you could say that now the fun begins. He continued to teach Agrostology each fall for four years. He continued to collect plants for his research and for the OSU herbarium. He had hoped to reach 10,000 collections before his collecting days are over, but it doesn't look like that will happen. (He is currently just above 6,250 and all who have seen his specimens will say, he goes for quality.) He wrote articles for amateur botanists that appeared in *Douglasia*, *Kalmiopsis*, and *Bulletin of the Native Plant Society of Oregon*. Many of the popular articles concern nomenclature, and his choice of titles ("Plants can change their names," "How to make a genus disappear," "Rare butterfly - rare plant," "A pesty weed and a botanical joke," and "Learn the gender of your genera") show that he has fun writing them. Another major retirement project is the Oregon Flora Project, of which he is a Checklist Project Leader. He has already completed treatments for most of the Asteraceae and all of the Berberidaceae, Campanulaceae, Linaceae, and Solanaceae.

In 1995, Ken took part in a symposium, "On the Occasion of the 100 Anniversary of the Birth of Göte Turesson," at AAAS, Pacific Division meetings in Santa Barbara. His paper, "The Contributions of Göte Turesson to Plant Taxonomy," was published in 1995 in the *Proceedings of the 73rd Annual Meeting.*

In addition to floristic, rare plant, and professional society work, Ken's retirement also includes non-botanical fun. Although he continues to read many science and botanical journals, he has time for other subjects too. He went on a Mayan "kick" a few years ago and read many books about that fascinating culture. He is a Gilbert and Sullivan aficionado and is building up a library of books, CDs and videos. Unfortunately, he shuns fiction and will never read any of the wonderful novels or mysteries that I read.

Having put off his musical and other interests for years, upon retirement he jumped in with both feet. His interest in Gilbert and Sullivan (G & S) operettas goes back to his childhood when his mother gave him *A Treasury of Gilbert & Sullivan*, a wonderfully illustrated book with the major solos and choruses from each of the operettas. When our daughter was young, she liked to sit on the piano bench and sing with him when he played. It was she who encouraged him to try out for the OSU summer production of "Patience" in 1991. He was given the part of Major Murgatroyd which had some solo lines and several small ensembles. As you might say, "The rest is history!" In 1992, he was in the chorus of "The Pirates of Penzance" where he was a pirate and a policeman. Next came "The Gondoliers" where he played the pompous, comical Duke of Plazatore. He played King Gama, the Scottish king, in "Princess Ida" in the summer of 1994. Ken prefers not to remember the summer of 1995, when he was chosen to be in the chorus of "H.M.S. Pinafore." He had an unfortunate fall in rehearsal where the set was not quite finished, that is to say there were no railings on the ship. He ended up with a broken leg and had to be a spectator that summer. The cast and crew dedicated the show to him, and that soothed the pain a bit. He was really looking forward to the summer of 1996 when "Iolanthe" was to be the production. He was cast as Private Willis who has a wonderful solo that is sung as he marches across the stage in uniform shouldering a rifle. He was also in the chorus in the first act where the famous March of the Peers had very challenging choreography. His grandchildren really enjoyed seeing him in that musical. Ken was in the chorus of the last two Gilbert & Sullivan plays: "The Mikado" in 1997 and "The Pirates of Penzance" again in 1998. One of the really nice things about the involvement in the G & S has been the "fans" he has created among his botany colleagues and other friends at OSU, as well as our neighbors. They have come to the plays to see him and in the process have become lovers of G & S.

Kenton L. Chambers. 1989 photo from OSU Archives.

His poetic talents were awakened on a vacation tour in the British Isles in 1996 when he started to write limericks while riding on the bus between the tour attractions. He would give the tour director a new limerick each day, which she would read sometime during the bus ride. She didn't tell who was writing them, but several of the members of the group guessed that it was Ken. The following are two of the best.

ON SHEEP IN THE COTSWALDS

There once was a ram in Grasmere,
Who said to the farmer, "See here,
The wool you may hack
From my sides and my back,
But be careful when shearing my rear!"

The farmer said, "Oh do not fear,
I'll steer clear of what's in the rear,
You needn't be nervous,
I'll keep you in service."
To which all the ewes cried, "Hear, hear!"

ON SCOTCH WHISKY

Now Scotland is known for its lochs,
And the funny way everyone talks.
To help you survive
And keep body alive,
They make whisky that knocks off your socks!

Another facet of his musical side appeared in 1996, after the August performances of G & S. We were window shopping in downtown Corvallis on a Saturday afternoon, and he saw a baritone horn in a music store. He purchased it and began practicing. The fingering was still in his head, since he had learned to play the instrument in elementary school. He joined the Oregon Tuba Association and played, with 100 other tubas and baritones, in Christmas Carol Concerts the next two Decembers, a tradition at the Eugene downtown mall. In the summer of 1998, he joined the Corvallis Community Band which gave a concert at Central Park every Monday evening. A few years ago at Christmas time, Ken sang in an English Caroling group, and currently is singing in a madrigals group.

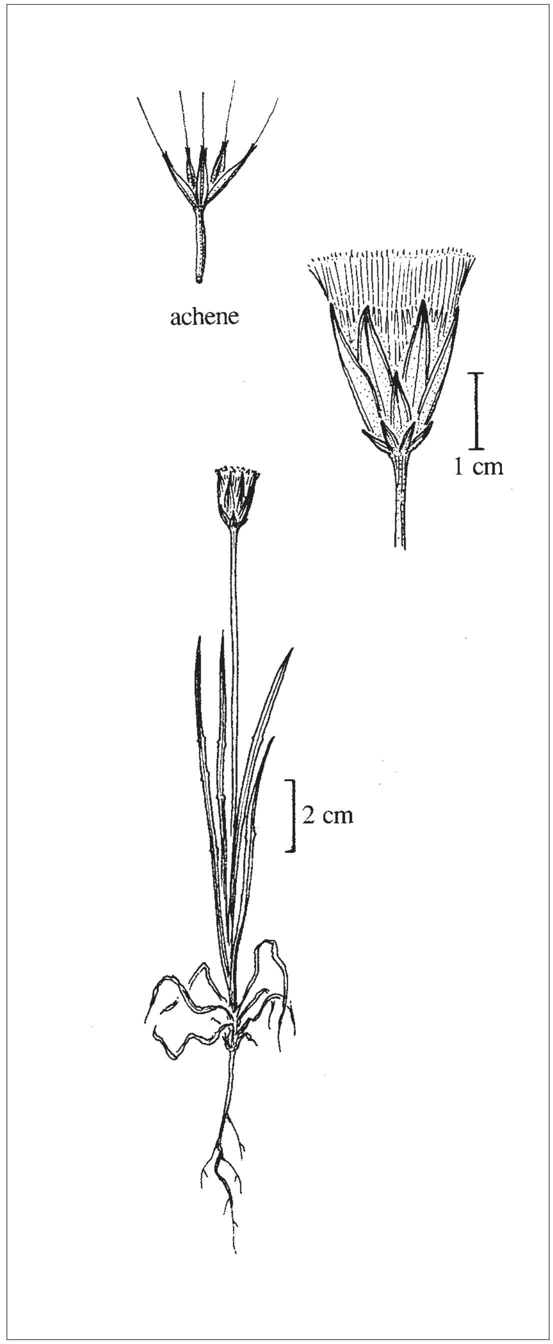
Ken inherited a collection of US postage stamps from his father in the late 1950s and has had great enjoyment filling in the holes and adding to it. This especially was fun after his children were out of college and on their own, and there was money to spend. He has specialized in mint singles, plate blocks and Zip blocks of commemoratives and airmails. Shortly after he retired, he entered all of his holdings into a data base so that the collection could be appraised. In late 1998 he decided that his interest in collecting was waning, and he donated his holdings of 1847-1931 stamps to the Oregon State University Foundation for an endowment fund for the Oregon Flora Project.

Our children, now adults, have both settled in the Portland area, and we are very fortunate that they live nearby. Elaine married William "Bill" Rea in 1989, and they are parents of two girls, Hayley and Holly. Ken really enjoys Bill, and they share interests in science, computers, stamps and many other things. David is a single parent with joint custody of his children, Brian and Melanie, and he is very involved in their lives. We try to have each of the grandchildren spend a week with us each summer, sometimes in Corvallis where they can attend day camp at OSU or at our cabin near Camp Sherman. Both Elaine and Dave inherited their musical interest and talent from their father. Elaine played the bassoon, and Dave still plays Ken's old trombone (as well as a newer one!) in professional jazz and rock groups in Portland. Ken is teaching our grandson Brian to play the ukulele, and I am sure that they soon will be playing together.

Acknowledgements

I would like to thank William L. Stern and Harry Thompson for their contribution to this biography.

Henrietta Laing Chambers and Ken have been married since 1958. She received her PhD from Yale in 1961 with Ken as her major advisor. Henny was a research assistant in Plant Pathology at OSU from 1961-1967 and a faculty member at Linn-Benton Community College from 1972-1988. She was associated with the National Clonal Germplasm Repository in Corvallis from 1988-1998 as the curator of the *Mentha* collection. She is co-author (with R.A. Ross) of *Wildflowers of the Western Cascades* (Timber Press, Portland. 1988).



Stebbinsoseris heterocarpa, drawn for A Flora of Santa Cruz Island (Junak *et al.* 1995) by Linda Ann Vorobik.

Editor's note: see Appendix I, Graduate Students of K. L. Chambers and their thesis titles, on p. 39, and Appendix II, Publications by K. L. Chambers, starting on p. 40.

Ken Chambers: Taxonomic Rigor and Rare Plant Protection in Oregon

Rhoda M. Love
393 Ful Vue Drive, Eugene, OR 97405

KEY WORDS: *Kenton L. Chambers, herbarium, Oregon Endangered Species Act, rare plant protection, taxonomy.*

Abstract. Kenton L. Chambers has played a major role in rare plant conservation in Oregon. After becoming Curator of the Oregon State University Herbarium in 1960 he almost at once began to catalogue the state's rare plant species. He and Jean Siddall were instrumental in organizing early state conferences which refined lists of Oregon's rare, threatened and endangered plants. His work was of key importance in the passage of the Oregon Endangered Species Act of 1987. Chambers's philosophy has consistently demonstrated that scientific understanding of taxonomy must precede and accompany conservation actions.

In January, 1999, the Native Plant Society of Oregon (NPSO) honored Kenton L. Chambers by naming him a Fellow of our Society—our organization's highest award. In my letter nominating Ken, I wrote, in part:

> *Ken's contribution to botany, both within and outside Oregon, has been so great since he came to our state in 1960, that one cannot put all the details in a single letter. Suffice it to say that a few of his accomplishments are: superb professor of botany, outstanding Herbarium Curator, impeccable taxonomic researcher, outstanding overseer of a large cadre of graduate students, earliest compiler of lists of Oregon's rare plant species, conservationist, contributor to the passage of the State Endangered Species Act, ... and, most especially, an accessible person who has never been too busy to promptly and fully answer the countless taxonomic questions that constantly come his way from all of us.*

In a note to me, responding to his nomination, Ken made the following informal observations (Chambers, pers. comm. 1999):

> *Over [Henny's and my] nearly 40 years in Oregon, this society (NPSO) has truly grown and prospered, with citizen involvement of a breadth and intensity that I could never have imagined back in the early '60s. There was a time, you know, when very few people knew or cared about the status of rare and endangered flora; mainly it was we professional taxonomists who could note and keep track of the diminishing number of populations of many wildflower species. Habitat alteration began to be really severe—I am thinking of my experience doing field work in central California—about the time I was doing my thesis work at Stanford. "In my lifetime" as it were, so many memorable stands of beautiful wildflowers have been destroyed in the California landscape. I have noticed it to a lesser extent in Oregon, and maybe the Endangered Species Act and state legislation has slowed the trend here. It is a wonderful benefit to the flora that the NPSO members around the state keep high their level of involvement with conservation in general and with organizations like the Nature Conservancy, which is also doing so much fine work.*

It is typical of Kenton Chambers that he modestly gives much of the credit for rare plant protection in Oregon to such groups as the Native Plant Society and The Nature Conservancy, credit both groups certainly deserve. Nevertheless, Chambers himself played a major role in conserving Oregon's endangered and threatened plants and their communities in the years since he arrived here as a young associate professor from Yale in 1960.

The Early Years: compiling lists for a foundation

In August 1960, Ken, his wife Henrietta, and their three-month-old daughter Elaine arrived in Corvallis, where he began his new post as associate professor of botany and curator of the Oregon State University (OSU) Herbarium. He soon familiarized himself with the herbarium as well as with the literature on Oregon plant taxonomy. The 1960s were, as we recall, a time of national awakening of interest in reversing the course of environmental degradation. Having seen the loss of plant habitat as a student in California, and hoping to prevent similar devastation in this state, Chambers began to compile a list of Oregon species which seemed to him to be rare. In his own words (Chambers 1997):

> *Prior to the U. S. Endangered Species Act of December 1973, I had prepared a preliminary list of Oregon rare plant species, focused especially on endemic taxa, which I gleaned from the standard reference floras such as Peck's* Manual of the Higher Plants of Oregon*, floras of adjacent states, research literature in higher plant taxonomy and the 'rarity' of numerous Oregon species in herbarium collections.*

Concurrently, Jean Siddall, a dedicated conservation activist and amateur botanist living at Lake Oswego, independently began a list of Oregon rare plants at the request of the Pacific Northwest Research Natural Area Committee (of the State Land Board), for the purpose of determining the research natural area needs of Oregon and Washington. Siddall based her list primarily on current field information gathered from amateur and professional botanists throughout the state. When Siddall and Chambers found they were listing many of the same species using two different methods, they combined efforts (Siddall *et al*. 1979, Love 1991).

It is obvious from Chambers's recollections of those early times that from the outset he wished to emphasize that a solid taxonomic foundation is essential for any legitimate conservation action (Chambers 1997):

> *Jean and I met several times to review my list and lists which she had prepared on her own, adding species which she felt were becoming rare through threats from human activities of various kinds. Her suggestions were based on her own field work in various parts of the state ... and on consultations with other Portland-area botanists, especially members of the Native Plant Society of Oregon. We thrashed out the many difficult questions that necessarily came up during these early stages of trying to identify and list all possible endangered species. I was more familiar with the botanical aspects of rarity—questions of the validity of taxonomic differences, patterns of endemism and its environmental correlations, how one might define species, varieties, and subspecies, which taxonomic references were more reliable, which botanists' taxonomic work could best be relied on, what use could be made of herbarium records, and so forth.*

In 1973, public concern about environmental damage and loss of biodiversity finally culminated in the passage of the Federal Endangered Species Act which protected plants as well as animals. The Act gave the Smithsonian Institution the responsibility for assembling a national list of threatened and endangered species. The first Smithsonian Report was published by the U.S. Fish and Wildlife Service in the *Federal Register* of July 1, 1975. Ken found the initial federal list of Oregon endangered plants "highly unsatisfactory." In response, Chambers and Siddall combined the federally-listed Oregon plants with their own much more comprehensive list to produce the *Provisional List of Rare, Threatened and Endangered Plants of Oregon*—568 species—which was published as "plants of special interest" in *Research Natural Area Needs in the Pacific Northwest* by C. T. Dyrness *et al*. (1975).

In late 1975, with the support of then Oregon Governor Robert Straub, a 12-member interagency Oregon Rare and Endangered Plant Species Task Force was formed. Its four goals were to (1) compile a list of rare, threatened and endangered plants in Oregon, (2) coordinate the gathering of information as a cooperative effort, (3) write status reports for species that should be listed nationally, and (4) assist in writing more comprehensive legislation for the protection Rare, Threatened and Endangered (RT&E) species in Oregon. In 1976 the Task Force organized a conference to review the species on the Provisional List, which was attended by 93 botanists from colleges, universities, agencies, and organizations throughout Oregon. They reviewed individually each of the 568 species on the Provisional List, discussing rarity and threats, annotating maps, and adding over 100 new species. Follow-up conferences were held in 1977, 1978 and 1979. Ken's colleague, Dr. Robert Frenkel of the OSU Department of Geography, was another important participant in these early conferences. By the third conference, the number of proposed species had grown to 686 and the number of participating botanists to well over 300.

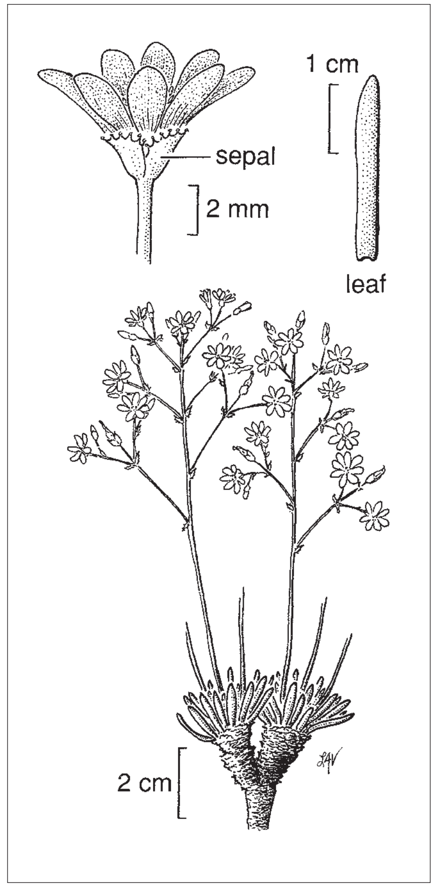
In addition to his contributions to these conferences, Chambers continued to research rare species by collating information from 25 herbaria across the country, adding substantial information regarding the historical ranges of the species. Many original collecting sites in Oregon were revisited in 1977 when Siddall distributed 816 field-checking assignments to botanists throughout the state. (My personal task was to check for *Lomatium bradshawii* near Nielsen Road in west Eugene. The species is there, but I failed to find it!) Chambers also directed OSU students who surveyed the literature and duplicated relevant sections of monographic revisions and technical articles, including descriptions, illustrations, and abstracts of range and habitats from various floras. With assistance from David Wagner (University of Oregon Herbarium), Chambers verified taxonomic identifications of doubtful herbarium records. Jean Siddall directed a corps of volunteers in Portland who compiled and transcribed the data from these sources.

By June 1979, it was time to review the Provisional List and determine which taxa should be formally listed, which dropped from further consideration, and which retained on a Review List. The results were published as *Rare, Threatened and Endangered Vascular Plants in Oregon—An Interim Report* by Siddall, Chambers, and Wagner, published by the Oregon Natural Area Preserves Advisory Committee to the State Land Board, Salem, October 1979. The primary list of 395 species, subspecies, and varieties, was supplemented by 130 review species. Amazingly, 38 listed taxa were not yet in the floras of the region. Oregon was the first state to produce such a comprehensive report, and Chambers's careful attention to taxonomic and historic detail imparted high credibility to the Interim Report.

In 1980, graduate student Bob Meinke of Corvallis, working under Ken's supervision in the OSU Herbarium, began a project to provide the Oregon rare plant data to field botanists, especially agency land managers. His work culminated in the 1982 book, *Threatened and Endangered Vascular Plants of Oregon: An Illustrated Guide,* funded by the U.S. Fish and Wildlife Service with assistance from the Forest Service, Bonneville Power Administration, Bureau of Land Management, and the Army Corps of Engineers. The

Curry County botanist Veva Stansell studying the hairy manzanita, *Arctostaphylos hispidula,* threatened or endangered in Oregon, found sparingly on serpentine soils in Curry, Douglas and Josephine counties. Photo by Charlene Simpson.

book included data, maps and illustrations of all rare species listed for Oregon in the *Federal Register* of December 15, 1980. In his acknowledgments Meinke thanked individuals who contributed unselfishly of their time and expertise in the preparation of the text. First on his list was Dr. Kenton Chambers, "who offered critical advice and the use of personal plant species files." Several other of Chambers's graduate students also worked on rare plants, including Carolyn Wright (*Astragalus diaphanus* var. *diaphanus,* JOHN DAY MILK VETCH), Nancy Fredricks (*Calochortus*, including the new species *C. umpquaensis,* UMPQUA MARIPOSA LILY), and Bob Meinke (*Mimulus,* with new species of such limited distribution that they remain on current rare species lists).



Lewisia leana, Lee's lewisia or quill-leaved lewisia. The species is stable in California but rare in Oregon where it is known from Douglas, Jackson and Josephine counties. Drawing by Linda Ann Vorobik from *The Jepson Manual*, © UC Press and the Jepson Herbarium, University of California.

Legislation in Oregon

When I became President of the Native Plant Society of Oregon in June 1982, my involvement with Oregon's rare species had consisted of attending several of the conferences in the 1970s and (unsuccessfully) searching for *Lomatium bradshawii* (BRADSHAW'S DESERT PARSLEY) in 1977. During my research for a PhD in plant ecology at the University of Oregon, my time was fully occupied. However, I now was ready to plunge into the effort to protect the species listed in the Interim Report. The major goal of my presidency was announced to NPSO members in our Society's Bulletin (Love 1982):

> *The major specific goal I would hope we can accomplish by 1984 is to see through the Oregon Legislature a bill protecting our state's rare native plants. This will not be easy and I will need the help of all our members. Our legislators will, in 1983, have the formidable task of balancing Oregon's budget, yet we must make our representatives in Salem see that protection of our threatened flora is a must if our state is to retain its leadership in environmental concerns. We must start early and work hard for the legislation we need to halt ... exploitation of our plants.*

Gentiana setigera, Waldo gentian, an ONHP List 1 species (endangered or threatened throughout its range), is part of the pitcher plant (*Darlingtonia californica*) bog community in Curry and Josephine counties and northern California. As Chambers observed, "the[se] plants are extremely sensitive in terms of conservation requirements, ... due to the specificity of the habitat and need for an all-year source of spring water." Photo by Charlene Simpson.

With this goal in mind I appointed a Legislative chair at my first board meeting, and we solicited cooperation from other organizations also dedicated to passing an Oregon Endangered Species Act, such as the Portland Audubon Society and the Oregon Natural Resources Council.

NPSO and its sister groups had not moved quickly enough to draft a bill for the 1983 or for the 1985 legislature, but we learned a great deal from our efforts, and we were determined to make a major effort during the 1987 session. The new NPSO Legislative Chair, Esther Gruber McEvoy was dedicated to making an Endangered Species Act for Oregon happen in 1987 and, with the help of our allies, it did (McEvoy 1987). State Representative Carl Hosticka of Eugene proudly called its passage a "minor miracle."

The bill eventually passed unanimously in both the House and Senate, but encountered difficulties at first, and Chambers played a key role in sustaining it at crucial moments. By April of the 1987 legislative session, after hearings on the budget had almost killed the bill, it passed the Senate by a "squeaker" vote of 16 to 14 and moved to the House where it faced an even more hostile environment. In the House, the bill was assigned to the Agriculture, Forestry and Natural Resources Committee chaired by Representative Bernie Agrons of Klamath Falls, a retired Weyerhaeuser executive. Representative Agrons invited all those who opposed the bill to testify first in order to, as he stated, "lay the cards on the table." Fortunately for our side, House Speaker Vera Katz of Portland was a strong proponent of endangered species legislation and saw to it that the House proceedings were fair. Testimony on both sides was called and many within NPSO appeared during the Committee hearings, including Chambers on May 12, 1987. The full text of his testimony is presented here as a demonstration of his steadfastness throughout his history of rare plant advocacy in Oregon to the belief in his role to explicate and champion the link between fundamental taxonomy

May 12, 1987

House Committee on Agriculture, Forestry, and Natural Resources
H197C, State Capitol Salem, OR 97310

TESTIMONY FOR INCLUSION IN THE RECORD OF HEARINGS ON SB 533

The following comments are intended to address questions that may arise in the hearings, concerning the taxonomic categories (species, subspecies, and varieties) of plants in Oregon which could come under the proposed new provisions and amendments.

As a professional plant taxonomist and botanical research scientist, I wish to address the scientific aspects of plant classification as they pertain to plant species conservation and the study of endangered and threatened plants. Specifically, the question may be asked as to what plant groups might be considered "threatened or endangered" under SB 533, and how does the technical classification of plants affect their inclusion in the bill. Persons knowledgeable about biological classification understand that disagreements often exist among taxonomists as to what comprises a "species," "subspecies," or "variety." The term "variety" as a scientific category in botany is essentially equivalent to "subspecies," in standing for a distinct subset of populations within a recognized plant species. The distinctness is normally recognized by a combination of visible morphological differences plus a defined geographical range together with implied or observable ecological requirements. What are not included in the bill are cultivated varieties like those created by horticulturists or plant breeders; furthermore, only plants that are native to Oregon are included, not ones that were introduced by accident or human agency which have "run wild" in the state. To identify, describe, and name plant species, subspecies, and varieties is a matter for serious scientific research; it is not a frivolous activity to be engaged in by untrained or unqualified persons. Such research must stand up to objective scrutiny by qualified scientific reviewers, must be published in a professional journal, and must be validated by authentic specimens and a description of the analytical methods used. This complicated process helps ensure that scientific standards are adhered to by those whose research forms the basis for plant classification.

As a practicing taxonomist I can verify that differences in interpretation exist about calling particular plants species, subspecies, or varieties. The so-called "splitters versus lumpers" arguments are a natural part of taxonomy and will never be resolved to 100% agreement in all cases. Fortunately, this problem does not much affect endangered-species legislation (at either the federal or state level), because following the model of the federal Endangered Species Act, protection can be extended to an endangered plant regardless of whether it is formally named as a species, subspecies, or variety. The dominant scientific criteria for taxonomy are that a plant group be (1) naturally evolved, (2) distinctive in morphology and geography/ecology, (3) verified by valid published research, and (4) able to stand up to review by botanical professionals who are not "interested parties" in the research.

Because botanical research, like all of science, is a human endeavor, we cannot do better than to hold to the above standards and expect that errors will be detected and corrected. A basic philosophical point to endangered species legislation is that species will not simply be conserved, but rather that well-considered "recovery" actions will be undertaken to bring them back from the brink of extinction. If a plant species can successfully be "recovered," it might eventually be taken off the endangered list. Another point is that money and human resources will always be limiting, and that priority will have to be given to species that truly merit protection. If there are unanswered questions about the taxonomic validity of a particular species, subspecies, or variety, it may have to be given low priority for study and listing under the proposed law. This is what now happens, in practice, at the federal level. Expensive resources cannot, in practical terms, be expended on plant groups for which there is serious scientific doubt as to their taxonomic distinctness. This is not to say that errors may not have been made in the past. But society is gaining experience with endangered-species studies and legislation, and we are thereby becoming more sophisticated in evaluating the process and in regulating the expenditures of funds and human effort.

I appreciate the opportunity to add these remarks to the record of the hearings by the Committee.

Kenton L. Chambers, PhD
Professor of Botany and Curator of the Herbarium

Lewisia cotyledon var. *purdyi*, Purdy's lewisia, is limited to serpentine soils in Curry and Josephine counties. It is on ONHP List 1, as well as a Federal taxon of concern and a candidate for State listing. Photo by Charlene Simpson.

Calochortus howellii, Howell's mariposa lily, is on ONHP List 1. Limited to Curry and Josephine counties, it was named for Oregon pioneer plant collector Thomas Jefferson Howell. Chambers's former graduate student Nancy Fredricks studied its ecology. Photo by Charlene Simpson.

and effective conservation efforts.

Continuing Defense of Rare Plants

Chambers's advocacy for rare plants continues as a personal endeavor, as well as through former graduate students, e.g., Bob Meinke, who oversees the Oregon Department of Agriculture program (Love 1998). For example, Chambers joined other members of NPSO to urge the agencies to protect a unique botanical assemblage at

March 18, 1993

Rochelle Desser
Illinois Valley Ranger District
Cave Junction, OR 97523

Dear Ms. Desser,

This letter is addressed to you at the suggestion of Anita Seda, District Botanist, who sent me a notice of the opportunity for comment on the proposed Wild and Scenic eligibility for Rough & Ready Creek. I would like to comment especially on the botanical features of the area, with emphasis on the plant species which have been noted as rare, endangered, or unusual in one context or another. My credentials are that I was for 30 years the Curator of the Herbarium at Oregon State University, and was a Professor of Botany there; also, I have been involved as a taxonomic advisor and consultant to botanists of the U.S. Forest Service for many years. My work on behalf of the botanical programs in Region 6 was recognized by an award at the annual meeting of Region 6 botanists at Hood River a few years ago.

Rough & Ready Creek has exceptional botanical interest due to its being in the heart of the upper Illinois River Valley, which is a center for endemic species of vascular plants. Endemism of plants implies a limited occurrence, correlated with a particular geographic region and/or with specific habitat conditions. The serpentine soil (peridotite rock) formations of the Illinois River region are believed to be a strong factor in limiting the distribution and occurrence of many plant species. Much plant physiological research has shown that only through particular specialized adaptations can plants live in strongly serpentinized soil. In many plant genera we observe that some species are never found on serpentine while other species are almost entirely limited to that soil substrate. The latter "serpentine endemics" often are local in occurrence and rare over their geographical range. Such is the case with numerous plants of the Rough & Ready Creek area.

The information I have on plants of that area comes from personal observations as a practicing plant taxonomist and field botanist, as well as from studies of herbarium specimens (plant collections) made by other botanists and preserved in the Oregon State University and University of Oregon herbaria. Also, I have read research reports and publications dealing with various plant species of the region. A graduate student of mine, Dr. Nancy Fredricks, did an ecological study of *Calochortus howellii*, a species of the Illinois River region, and wrote her doctoral thesis this past December, 1992. My personal research has involved the taxonomy of a species of family Asteraceae (*Microseris howellii*), which is endemic to the Illinois River Valley, and I have studied two related species of *Microseris* in the same area. A former student of mine, Dr. Leslie Gottlieb, did his Masters Degree thesis research on hybridization between two species of *Arctostaphylos* (manzanita) found in the same region.

I have prepared the attached list of plant species of special interest, which are either known to occur near Rough & Ready Creek or are highly likely to be found there; these are selected from the lists of plants in the publication "Rare, Threatened, and Endangered Plants and Animals of Oregon," May 1991 edition, produced by the Oregon Natural Heritage Program of The Nature Conservancy, Portland, Oregon. This is not a list of all of the plants of the area, of course, but is a selection of those which are on one of the State of Oregon lists—either as "endangered or threatened throughout their range" (List 1), "endangered or threatened in Oregon, more common or stable elsewhere" (List 2), or "species of concern which are not currently threatened or endangered" (List 4). Further botanical exploration is very much needed, due to the richness of the flora of Rough and Ready Creek area; such exploration may add more names to these lists, of plants not previously verified as being in that exact area although known from nearby regions.

Some of the above-listed species are of particular interest as members of the plant community defined by permanently wet hillside seeps and bogs. A species of PITCHER PLANT, *Darlingtonia californica,* is diagnostic of this habitat; the plants are extremely sensitive in terms of conservation requirements, due to their being overharvested in the past for commercial sale, and due as well to the specificity of the habitat and need for an all-year source of spring water. *Gentiana setigera* and *Cypripedium californicum*, along with other interesting bog plants such as BUTTERWORT, *Pinguicula vulgaris,* occur with the *Darlingtonia.*

Another botanical feature of the Rough & Ready Creek area that is of interest from a genetic and evolutionary standpoint is the presence of natural hybridization between species in two common shrubby genera, *Arctostaphylos* and *Ceanothus* (manzanita and deer brush). In *Arctostaphylos*, hybridization between *A. viscida* and *A. canescens* has produced a large stand of more-or-less intermediate plants on the gravelly flood-plain of the upper Illinois River near the confluence of Rough & Ready Creek (my personal observations). Similar hybrids were studied by Leslie Gottlieb at the nearby old mining town of Waldo (published in Brittonia, Vol. 20, pgs. 83-93, 1968). These intermediate plants of hybrid origin can be assigned the "hybrid species" name *Arctostaphylos* X *cinerea* Howell; they were first described by Thomas Howell, in 1901, as a true species but according to Gottlieb are to be considered a hybrid swarm that has not yet stabilized to become a genetic species. In the second-mentioned genus, *Ceanothus*, hybridization between *C. cuneatus* and *C. pumilus* has been reported from the Rough & Ready area. Preliminary observations were published by Malcolm Nobs in 1963 (see: Carnegie Institution of Washington, Publication 623, pg. 77). These hybrids have not been given a technical name as yet. Their occurrence is probably sporadic and related to disturbance of the natural habitat by human activities (according to Nobs, above). However, the origin of new species through hybridization between existing ones is known to be an evolutionary process in both *Arctostaphylos* and *Ceanothus*, so the presence of the interspecies hybrids just mentioned is of special interest as a unique botanical feature of the region being considered for Wild and Scenic eligibility.

I will not be available to attend the public meeting scheduled for March 29, 1993. If I can provide more information and/or written materials regarding the plants and botanical features described above, please let me know. Thank you for the opportunity to provide input into your proceedings.

Sincerely,

Kenton L. Chambers
Emeritus Professor of Botany & Plant Pathology

Triteleia hendersonii var. *leachiae*, Leach's brodiaea, is on ONHP List 1 and is a candidate for State listing. Named for two of Oregon's best-known plant collectors, Louis F. Henderson and Lilla Leach, this lovely member of the lily family grows in Coos and Curry counties. Photo by Charlene Simpson.

Rough and Ready Creek in southern Josephine County, a flora adapted to the mineral-laden serpentine substrate. I quote his letter in full below.

Rational, accurate and taxonomically sound, this letter concludes my essay on Ken Chambers's ongoing involvement with rare plant protection in Oregon. Chambers has always felt that the best argument for preservation is scientific, and he is a master at arguing his case based on the best taxonomic evidence. Even in "retirement," he maintains a major role in plant conservation in our state. His present work on the new *Flora of Oregon* reflects a continuation of

Rare Plants of the Rough and Ready Creek Area

Plant species of List 1, "Endangered or Threatened Throughout their Range":
[Common names added by editors.]

Calochortus howellii (Lily Family)
Howell's mariposa-lily[1]
Gentiana setigera (Gentian Family)
Waldo gentian
Lewisia cotyledon var. *purdyi* (Purslane Family)
Purdy's lewisia
Hastingsia bracteosa (Lily Family)
purple or largeflower rushlily
Limnanthes gracilis (Meadowfoam Family)
slender meadow-foam
Microseris howellii (Sunflower Family)
Howell's microseris
Triteleia hendersonii var. *leachiae* (Lily family)
Leach's brodiaea
Senecio hesperius (Sunflower Family)
Western senecio
Viola lanceolata subsp. *occidentalis* (Violet Family)
Western lance-leaved violet

[1] Common names from: Mullens, L. 2000. A Guide to Rare Plants of the Siskiyou National Forest. USDA Forest Service, Grants Pass, Oregon.

Plant species of List 2, "Endangered or Threatened in Oregon, more common or stable elsewhere":

Arctostaphylos hispidula (Heath Family)
hairy manzanita
Epilobium rigidum (Evening-primrose Family)
rigid willow-herb
Erythronium howellii (Lily Family)
Howell's adder's-tongue
Fritillaria glauca (Lily Family)
Siskiyou fritillary
Lewisia leana (Purslane family)
Lee's lewisia
Lomatium engelmannii (Carrot Family)
Engelmann's desert parsley
Lomatium tracyi (Carrot Family)
Tracy's lomatium
Monardella purpurea (Mint Family)

SISKIYOU MONARDELLA
Sanicula peckiana (Carrot Family)
PECK'S SNAKE-ROOT
Salix delnortensis (Willow Family)
DEL NORTE WILLOW
Salix tracyi (Willow Family)
TRACY'S WILLOW
Sedum laxum subsp. *heckneri* (Stonecrop Family)
HECKNER'S STONECROP

Plant species of List 4, "Species of Concern which are not currently threatened or endangered":

Arabis aculeolata (Mustard Family)
WALDO ROCK CRESS[2]
Arenaria howellii (Chickweed Family) HOWELL'S SANDWORT
Balsamorhiza sericea (Sunflower Family)
SILKY BALSAMROOT
Cypripedium californicum (Orchid Family)
CALIFORNIA LADY'S SLIPPER
Darlingtonia californica (Pitcher-plant Family)
CALIFORNIA PITCHER-PLANT
Dicentra formosa subsp. *oregana* (Fumitory Family)
OREGON BLEEDING-HEART
Eriogonum pendulum (Knotweed Family)
NODDING BUCKWHEAT
Eriogonum ternatum (Knotweed Family)
WALDO BUCKWHEAT
Lewisia oppositifolia (Purslane Family)
OPPOSITE-LEAVED LEWISIA
Lewisia cotyledon var. howellii (Purslane Family)
IMPERIAL LEWISIA
Streptanthus howellii (Mustard Family) HOWELL'S STREPTANTHUS
Thlaspi montanum var. *siskiyouense* (Mustard Family) SISKIYOU PENNY-CRESS

[2] Common names from Oregon Natural Heritage Program. 1993. Rare, Threatened and Endangered Plants and Animals of Oregon. Portland, Oregon.

his philosophy that understanding the native flora—in all its elusive detail and intricacy—must always be the first step in protecting this priceless botanical legacy.

Acknowlegements

I thank Henrietta L. Chambers for biographical material and Esther Gruber McEvoy for a copy of Kenton Chambers's May 12, 1987, testimony before the House Agriculture and Natural Resources Committee. I also thank Clay Gautier for assistance with scanning and Charlene Simpson for providing photographs of rare plants of southwest Oregon.

References

Chambers, K. L. 1997. Jean Siddall, biographical memoir. Unpublished remarks made at the June 3rd memorial service for Jean Siddall (1930-1997) in Portland.

Chambers, K. L. 1999. Unpublished January 27th e-mail to Rhoda Love, re: public interest in endangered species.

Dyrness, C.T., J. F. Franklin, and C. Maser. 1975. Research natural area needs in the Pacific Northwest: a contribution to land-use planning. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland.

Love, R. M. 1982. Greetings from the New President. Bulletin of the Native Plant Society of Oregon 5(6):1.

Love, R. M. 1991. A brief history of rare plant protection in Oregon. P. 37 in Oregon Natural Heritage Program, August. Rare, threatened and endangered plants and animals of Oregon. A cooperative project of The Nature Conservancy and the State of Oregon. 1205 N.W. 25th Avenue, Portland.

Love, R. M. 1998. Rare plants and the Oregon Flora Project. Oregon Flora Newsletter 4(1):4.

McEvoy, E. G. 1987. The legislative history of the Oregon State Endangered Species Act of 1987. Bulletin of the Native Plant Society of Oregon 20(8):78-79.

Meinke, R. J. 1982. Threatened and endangered vascular plants of Oregon: an illustrated guide. Especially page vii, Acknowledgments. US Fish and Wildlife Service, Office of Endangered Species, Region 1, Portland.

Oregon Natural Heritage Program. 1991. Rare, threatened and endangered plants and animals of Oregon. A cooperative project of The Nature Conservancy and the State of Oregon.1205 N. W. 25th Avenue, Portland.

Siddall, J. L., K. L. Chambers, and D. H. Wagner. 1979. Rare, threatened and endangered vascular plants in Oregon—an interim report. Pp. 5-8, History of the Oregon rare and endangered plant project. Oregon Natural Area Preserves Advisory Committee to the State Land Board, Salem.

Rhoda M. Love (MS, University of Washington; PhD, University of Oregon) was a botany instructor at Lane Community College for nearly 30 years. She taught the spring course in systematic botany at OSU for two semesters, filling in during Ken Chambers's absences. Now retired, she was until recently Secretary of the Native Plant Society of Oregon. She also volunteers with the Oregon Flora Project and serves as editor of the *Oregon Flora Newsletter.*

Flora of Walker Flat, Yamhill County, Oregon

Richard R. Halse
Herbarium, Department of Botany and Plant Pathology
Oregon State University, 2082 Cordley Hall, Corvallis, OR 97331-2902

Judith B. Glad
Botanical Consultant, 4969 S.E. 133rd Drive,
Portland, OR 97236-3967

KEY WORDS: *flora,* Sidalcea nelsoniana, *Walker Flat, Yamhill County, Oregon.*

Abstract. Walker Flat is an upland meadow-wetland complex in the Coast Range of Yamhill County, Oregon. A list of extant plant species was compiled between 1985 and 1998, including bryophytes and vascular plants. The flora comprises 259 species with representatives of 181 genera and 73 families.

Walker Flat is an upland meadow-wetland complex along Walker Creek, a tributary of the Nestucca River, in Yamhill County, approximately 40 ha in extent. Intermittently grazed during the first half of the 20th century, it has lain fallow for a number of years, used only by occasional recreationists and hunters. Intermingled conifer forest and riparian mixed woodlands surround it. Wetland elements are scattered throughout grass meadows and along the tributaries and main stem of Walker Creek. These plant associations range from a relatively dry *Scirpus microcarpus-Lupinus polyphyllus* (SMALL-FRUITED BULRUSH-BIGLEAF LUPINE) community to a permanently wet *Carex utriculata-Viola palustris* (BEAKED SEDGE-MARSH VIOLET) association. Scattered clumps of shrubs, e.g., *Crataegus* (HAWTHORN), *Symphoricarpos* (SNOWBERRY), *Rosa* (ROSE) interrupt the dominance of introduced grasses across the meadows. *Salix* spp. (WILLOW) grow sporadically along the creeks and in thickets at some wetland edges. Patches of conifer forest sometimes extend into the meadows, and lobes of grassland and sedge marsh reach some distance into both conifer forest and riparian woodland. *Lysichiton americanum* (SKUNK CABBAGE) sometimes grows in the understory of riparian woodlands (Glad *et al*. 1987).

Walker Flat ranks among the larger upland meadow-wetland complexes in the Coast Range, although it is not the largest nor the least disturbed. Grazing, logging of adjacent forests, road construction, and recreational use have altered the topography and vegetation. Species composition is fairly typical of complexes with a similar history (CH2M HILL, Inc. 1990a).

Walker Flat was grazed until the 1950s (J. Nicholls, McMinnville, Oregon, pers. comm.). The original Bald Mountain Road cut through the west meadow. Roadside ditches are still evident, and traces of the road itself can be detected on aerial photographs. Hillsides surrounding Walker Flat have been logged since 1985; most of the timber removed was second growth, testifying to early logging in the area. For a number of years, ending in the early 1980s, the west meadow was used by recreational motorcyclists. Aerial photographs taken in 1979 show clear trails through the grass and circling some of the larger shrub clumps. This human activity introduced exotic plants, particularly in the meadows.

Walker Flat was heavily utilized by Roosevelt elk (Bureau of Land Management 1985) until the surrounding forests were logged in the early 1990s. After that, elk use decreased and shrubs in the meadows, which had been suppressed, began to spread. Since 1990, considerable growth of existing shrubs has led to canopy closure over some of the meadows (CH2M HILL, Inc. 1997).

The northern (lower) end of Walker Flat is a mosaic of open-water and palustrine wetlands that remain flooded in all but the driest of summers. Beaver periodically have dammed Walker Creek upstream of the culvert at the lower end. Sometimes these beaver dams have been wholly or partially washed away, causing changes in surface water hydrology along the creek. No major species shifts have been seen in these areas, probably because the flooding and draining have been short term.

McMinnville Water and Light Department, owner of approximately two-thirds of the area, planned to build a dam on Walker Creek, flooding Walker Flat. Utility-instituted environmental studies at Walker Flat between 1983 and1986 were supplemented during site visits in the ensuing years (Bureau of Land Management 1985 and CH2M HILL, Inc. 1986 - 1997).

Discovery of the rare *Sidalcea nelsoniana* (NELSON'S CHECKERMALLOW) by the Bureau of Land Management (BLM) at Walker

Richard and Judith were Ken Chambers's graduate students in the early 1970s. This article, fruit of their work in western Oregon, is offered as a tribute to their mentor during their graduate studies. About Ken Chambers as a major professor, Judith states, "Ask any grad student. Major professors can make your life miserable, can drive you crazy, can nit-pick you to death. Of course, there are those who support and encourage you, easing your way through one of the more difficult passages of your life. Fortunately, Ken Chambers was one of the latter, and he did that for both of us. A fine teacher, an understanding mentor, and a gentle man, he stands far above the ordinary. And he does Gilbert and Sullivan so well, too!"

Typical growth form and habitat of *Sidalcea nelsoniana* in western Oregon. Photo by Richard Halse.

Flat in 1983 led to more intensive studies of its habitat and abundance. Despite thorough searches of the Oregon Coast Range and the Willamette Valley, the Walker Flat population of *S. nelsoniana* remains the largest known. *Sidalcea nelsoniana* was designated a threatened species by both the State of Oregon (Oregon Department of Agriculture 1989) and the Federal government (Federal Register 1993). McMinnville Water and Light conducted studies at Walker Flat through 1997. Additional studies conducted on the BLM-managed portion of Walker Flat by the BLM (1985) and Guerrant (1997) primarily addressed the abundance and survival of *S. nelsoniana* and the more abundant of its associated species. Ballot Measure 7 was passed in 1988, designating Walker Creek a Scenic Waterway, including Walker Flat.

A plant species inventory of Walker Flat began in 1985, along with environmental monitoring and plant community mapping (Bureau of Land Management 1985, CH2M HILL, Inc. 1986). Collection and identification of bryophytes and vascular plants at Walker Flat continued through the 1998 growing season. During some years the site was visited in spring, summer and fall. Vouchers were collected for most of the taxa, except for exotic species and common, easily recognized native species. Voucher specimens are deposited at Oregon State University Herbarium (OSC) in Corvallis.

Nomenclature was derived from a variety of sources. Liverworts follow Stotler and Crandall-Stolter (1977); mosses, the *Checklist of Oregon Mosses* (Christy *et al.* 1982); ferns, fern allies, and conifers, *The Flora of North America*, volume 2 (Flora of North America Editorial Committee 1993); Magnoliophyta, primarily the *Flora of the Pacific Northwest* (Hitchcock and Cronquist 1973), excepting the Asteraceae follows Chambers and Sundberg (1998); additionally, *The Jepson Manual* (Hickman 1993) was used for nomenclatural updates. When other sources were used, the appropriate synonym from Hitchcock and Cronquist (1973) follows in brackets. Following each scientific name is a common name, based on Hitchcock and Cronquist when possible.

Two hundred fifty-nine plant species have been found at Walker Flat. Bryophytes comprise nearly a fourth of the families represented, but only about 10% of the species (Table 1). Over half of the families and 60% of the species are dicots. Two families, Poaceae and Asteraceae, comprise almost one-fourth of the extant

Table 1. The number of families, genera and species represented in the flora of Walker Flat, Yamhill County, Oregon.

TAXON	FAMILIES	GENERA	SPECIES
Bryophyta	17	23	27
Ferns & Fern Allies	6	7	8
Coniferophyta	1	3	3
Magnoliopsida	40	108	153
Liliopsida	9	40	68
TOTAL	73	181	259

Perfect flowers of *Sidalcea nelsoniana*. Photo by Richard Halse.

Table 2. The number of genera and species in largest families in the flora of Walker Flat, Yamhill County, Oregon.

FAMILY	GENERA	SPECIES
Poaceae	21	30
Asteraceae	22	29
Rosaceae	12	17
Cyperaceae	3	13
Ranunculaceae	4	9
Juncaceae	2	9
Liliaceae	6	8
Fabaceae	4	8

plant species, and with six other families, account for more than half of all vascular plant species (Table 2).

There are ten species of *Carex* (SEDGE) in the flora, more than in any other genus. Six species of *Juncus* (RUSH) and five each of *Festuca* (FESCUE) and *Ranunculus* (BUTTERCUP) are present.

The history of use at Walker Flat explains the abundance of exotic plant species. There are 43 species of exotics, about 20 percent of all flowering plants. No exotic bryophytes, conifers, ferns or fern allies have been found.

Further work at Walker Flat will undoubtedly list additional species; however, the majority of extant taxa are included. An asterisk indicates exotic taxa.

Walker Flat. Walker Creek in February. Photo by Richard Halse.

The Flora

BRYOPHYTA (Bryophytes)

Hepaticopsida (Liverworts)

JUBALACEAE
Frullania nisquallensis Sull.
LOPHOCOLEACEAE
Chiloscyphus polyanthos (L.) Corda
PORELLACEAE
Porella navicularis (Lehm. & Lindenb.) Pfieff.
SCAPANIACEAE
Scapania bolanderi Austin

Muscopsida (Mosses)

AMBLYSTEGIACEAE
Calliergonella cuspidata (Hedw.) Loeske
AULACOMNIACEAE
Aulacomnium androgynum (Hedw.) Schwägr.
BRACHYTHECIACEAE
Brachythecium frigidum (Mull. Hal) Besch.
Eurhynchium oreganum (Sull.) A. Jaeg.
Isothecium stoloniferum Brid.
DICRANACEAE
Dicranum howellii Renauld & Cardot
DITRICHACEAE
Ditrichum sp.
FONTINALACEAE
Fontinalis neomexicana Sull. & Lesq.
GRIMMIACEAE
Racomitrium heterostichum (Hedw.) Brid.
HYLOCOMIACEAE
Hylocomium splendens (Hedw.) Schimp.
Rhytidiadelphus loreus (Hedw.) Warnst.
Rhytidiadelphus triquetrus (Hedw.) Warnst.
HYPNACEAE
Hypnum circinale Hook.
Hypnum subimponens Lesq.
LEUCODONTACEAE
Antitrichia curtipendula (Hedw.) Brid.
MNIACEAE
Leucolepis acanthoneuron (Schwägr.) Lindb.
Plagiomnium medium (B.S.G.) T. J. Kop.
Rhizomnium glabrescens (Kindb.) T. J. Kop.
ORTHOTRICHACEAE
Orthotrichum consimile Mitt.
Orthotrichum lyellii Hook. & Taylor
Ulota megalospora Ventun ex Röll
PLAGIOTHECIACEAE
Plagiothecium laetum Schimp.
Plagiothecium piliferum (Sw. ex Hartmann) Schimp.

EQUISETOPHYTA (Horsetails)

EQUISETACEAE
Equisetum arvense L. — COMMON HORSETAIL

Equisetum telmateia Ehrh. ssp. *braunii* (Milde) Hauke — GIANT HORSETAIL

POLYPODIOPHYTA (Ferns)

BLECHNACEAE

Blechnum spicant (L.) Smith — DEER-FERN

DENNSTAEDTIACEAE

Pteridium aquilinum (L.) Kuhn in Decker var. *pubescens* Underwood — BRACKEN

DRYOPTERIDACEAE

Athyrium filix-femina (L.) Roth ex Mertens var. *cyclosorum* Rupr. — LADY-FERN

Polystichum munitum (Kaulf.) Presl — SWORD-FERN

OPHIOGLOSSACEAE

Botrychium multifidum (Gmel.) Rupr. — LEATHERY GRAPE-FERN

POLYPODIACEAE

Polypodium glycyrrhiza D. C. Eat. — LICORICE-FERN

CONIFEROPHYTA (Conifers)

PINACEAE

Abies grandis (Dougl. ex D. Don in Lambert) Lindl. — GRAND FIR

Pseudotsuga menziesii (Mirbel) Franco — DOUGLAS-FIR

Tsuga heterophylla (Raf.) Sarg. — WESTERN HEMLOCK

MAGNOLIOPHYTA (Flowering Plants)

Magnoliopsida (Dicots)

ACERACEAE

Acer circinatum Pursh — VINE MAPLE

ANACARDIACEAE

Toxicodendron diversilobum (T. & G.) Greene [*Rhus diversiloba* T. & G.] — POISON OAK

APIACEAE

Angelica genuflexa Nutt. — KNEELING ANGELICA

**Daucus carota* L. — QUEEN ANNE'S LACE

Oenanthe sarmentosa Presl — PACIFIC WATER-PARSLEY

Osmorhiza chilensis H. & A. — MOUNTAIN SWEET-CICELY

Osmorhiza purpurea (Coult. & Rose) Suksd. — PURPLE SWEET-CICELY

Perideridia gairdneri (H. & A.) Math. ssp. *borealis* Chuang & Constance — GAIRDNER'S YAMPAH

ARALIACEAE

Oplopanax horridum (Smith) Miq. — DEVIL'S CLUB

Walker Flat. West meadow. Photo by Richard Halse.

Walker Flat. Meadow in September. Photo by Richard Halse.

ARISTOLOCHIACEAE

Asarum caudatum Lindl. — WILD GINGER

ASTERACEAE

Achillea millefolium L. — COMMON YARROW

Adenocaulon bicolor Hook. — PATHFINDER

Agoseris grandiflora (Nutt.) Greene — LARGE-FLOWERED AGOSERIS

Anaphalis margaritacea (L.) Benth. & Hook. — PEARLY EVERLASTING

**Anthemis cotula* L. — STINKING MAYWEED

Aster modestus Lindl. — FEW-FLOWERED ASTER

Aster subspicatus Nees — DOUGLAS' ASTER

**Bellis perennis* L. — ENGLISH LAWN DAISY

**Cirsium arvense* (L.) Scop. — CANADA THISTLE

Cirsium brevistylum Cronq. — SHORT-STYLED THISTLE

**Cirsium vulgare* (Savi) Tenore — BULL THISTLE

**Crepis capillaris* (L.) Wallr. — SMOOTH HAWKSBEARD

Gnaphalium palustre Nutt. — LOWLAND CUDWEED

Gnaphalium purpureum L. — PURPLE CUDWEED

**Gnaphalium uliginosum* L. — MARSH CUDWEED

Hieracium albiflorum Hook. — WHITE-FLOWERED HAWKWEED

**Hypochaeris radicata* L. — SPOTTED CATS-EAR

**Lactuca muralis* (L.) Fresen. — WALL LETTUCE

**Leontodon taraxacoides* (Vill.) Merat ssp. *taraxacoides* [*L. nudicaulis* (L.) Merat ssp. *taraxacoides* (Vill.) Schinz & Thell.] — HAIRY HAWKBIT

**Leucanthemum vulgare* Lam. [*Chrysanthemum leucanthemum* L.] — OXEYE-DAISY
Madia glomerata Hook. — CLUSTER TARWEED
Petasites frigidus (L.) Fries var. *palmatus* (Ait.) Cronq. — SWEET COLTSFOOT
Psilocarphus elatior (Gray) Gray — TALL WOOLLY-HEADS
**Senecio jacobaea* L. — TANSY RAGWORT
**Senecio sylvaticus* L. — WOOD GROUNDSEL
Senecio triangularis Hook. var. *triangularis* — ARROWLEAF GROUNDSEL
Solidago canadensis L. var. *salebrosa* (Piper) M.E. Jones — CANADA GOLDENROD
**Sonchus asper* (L.) Hill — PRICKLY SOW-THISTLE
**Taraxacum officinale* Weber ex Wigg. — COMMON DANDELION

BERBERIDACEAE
Achlys triphylla (Smith) DC. ssp. *triphylla* — VANILLALEAF
Berberis nervosa Pursh — DULL OREGONGRAPE
Vancouveria hexandra (Hook.) Morr. & Dec. — INSIDE-OUT-FLOWER

BETULACEAE
Alnus rubra Bong. — RED ALDER

BORAGINACEAE
**Myosotis discolor* Pers. — YELLOW-AND-BLUE FORGET-ME-NOT
Myosotis laxa Lehm. — SMALL-FLOWERED FORGET-ME-NOT

BRASSICACEAE
Barbarea orthoceras Ledeb. — AMERICAN WINTERCRESS
Cardamine breweri Wats. var. *orbicularis* (Greene) Detl. — BREWER'S BITTERCRESS
Cardamine occidentalis (Wats. ex Robins.) Howell — WESTERN BITTERCRESS
Cardamine pensylvanica Muhl. ex Willd. — PENNSYLVANIA BITTERCRESS
Cardamine nuttallii Greene var. *nuttallii* [*C. pulcherrima* (Robins.) Greene var. *tenella* (Pursh) Hitchc.] — SLENDER TOOTHWORT
Rorippa curvisiliqua (Hook.) Bessey ex Britt. — WESTERN YELLOWCRESS

CALLITRICHACEAE
Callitriche heterophylla Pursh — VARIABLE-LEAF WATER-STARWORT

CAMPANULACEAE
Campanula scouleri Hook ex DC. — SCOULER'S BELLFLOWER

CAPRIFOLIACEAE
Lonicera ciliosa (Pursh) Poir. ex DC. — ORANGE HONEYSUCKLE
Lonicera involucrata (Richards.) Banks ex Spreng. var. *involucrata* — BLACK TWINBERRY
Sambucus racemosa L. var. *arborescens* (T. & G.) Gray — RED ELDERBERRY
Symphoricarpos albus (L.) Blake var. *laevigatus* Fern. — COMMON SNOWBERRY

CARYOPHYLLACEAE
**Cerastium fontanum* Baumg. ssp. *vulgare* (Hartm.) Greuter & Burdet [*C. vulgatum* L.] — COMMON CHICKWEED
Moehringia macrophylla (Hook.) Fenzl [*Arenaria macrophylla* Hook.] — BIGLEAF SANDWORT
Sagina apetala Ard. — COMMON PEARLWORT
Sagina procumbens L. — PROCUMBENT PEARLWORT
**Spergularia rubra* (L.) J. & C. Presl — RED SANDSPURRY
Stellaria calycantha (Ledeb.) Bong. — NORTHERN STARWORT

CONVOLVULACEAE
Calystegia atriplicifolia Hallier f. ssp. *atriplicifolia* [*Convolvulus nyctagineus* Greene] — NIGHT-BLOOMING MORNING-GLORY

CORNACEAE
Cornus unalaschkensis Ledeb. [*C. canadensis* L. misapplied] — BUNCHBERRY

ERICACEAE
Gaultheria shallon Pursh — SALAL
Pyrola asarifolia Michx. var. *asarifolia* — ALPINE PYROLA
Vaccinium parvifolium Smith — RED BILBERRY

FABACEAE
Lotus aboriginus Jeps. [*L. crassifolius* (Benth.) Greene var. *subglaber* (Ottley) Hitchc.] — BIG DEERVETCH
Lotus purshianus (Benth.) Clements & Clements — SPANISH-CLOVER
Lupinus latifolius Agardh — BROADLEAF LUPINE
Lupinus polyphyllus Lindl. var. *polyphyllus* — BIGLEAF LUPINE
**Trifolium dubium* Sibth. — LEAST HOP-CLOVER
**Trifolium pratense* L. — RED CLOVER
**Trifolium repens* L. —WHITE CLOVER
Vicia americana Muhl. ex Willd. — AMERICAN VETCH

FUMARIACEAE
Dicentra formosa (Haw.) Walp. — PACIFIC BLEEDINGHEART

GROSSULARIACEAE
Ribes divaricatum Dougl. — STRAGGLY GOOSEBERRY

HYDROPHYLLACEAE
Hydrophyllum tenuipes Heller — PACIFIC WATERLEAF

Walker Flat. Central meadow in June. Photo by Richard Halse.

Walker Flat. West meadow. Photo by Richard Halse.

Nemophila parviflora Dougl. ex Benth. var. *parviflora* — SMALL-FLOWERED NEMOPHILA

HYPERICACEAE

Hypericum anagalloides C. & S. — BOG ST. JOHN'S-WORT

Hypericum formosum Kunth var. *scouleri* (Hook.) Coulter — WESTERN ST. JOHN'S-WORT

LAMIACEAE

Prunella vulgaris L. — SELF-HEAL

Stachys cooleyae Heller — GREAT BETONY

MALVACEAE

Sidalcea nelsoniana Piper — NELSON'S CHECKER-MALLOW

ONAGRACEAE

Epilobium angustifolium L. — FIREWEED

Epilobium glaberrimum Barbey — SMOOTH WILLOWHERB

OXALIDACEAE

Oxalis oregana Nutt. — OREGON OXALIS

Oxalis trilliifolia Hook. — GREAT OXALIS

PLANTAGINACEAE

**Plantago lanceolata* L. — ENGLISH PLANTAIN

**Plantago major* L. — COMMON PLANTAIN

POLEMONIACEAE

Collomia heterophylla Hook. — VARIED-LEAF COLLOMIA

Linanthus bicolor (Nutt.) Greene — BICOLORED LINANTHUS

Navarretia squarrosa (Esch.) H. & A. — SKUNKWEED

Phlox gracilis (Hook.) Greene [*Microsteris gracilis* (Hook.) Greene] — PINK MICROSTERIS

POLYGONACEAE

**Polygonum aviculare* L. — DOORWEED

**Rumex acetosella* L. — RED SORREL

**Rumex crispus* L. — YELLOW DOCK

**Rumex obtusifolius* L. — BITTERDOCK

PORTULACACEAE

Claytonia sibirica L. [*Montia sibirica* (L.) Howell] — WESTERN SPRINGBEAUTY

Montia fontana L. — WATER CHICKWEED

Montia linearis (Dougl. ex Hook.) Greene — NARROW-LEAVED MONTIA

PRIMULACEAE

Trientalis latifolia Hook. — WESTERN STARFLOWER

RANUNCULACEAE

Actaea rubra (Ait.) Willd. — BANEBERRY

Anemone deltoidea Hook. — THREELEAF ANEMONE

Anemone oregana Gray — OREGON ANEMONE

Aquilegia formosa Fisch. — RED COLUMBINE

Ranunculus alismifolius Geyer ex Benth. [*R. alismaefolius* Geyer] — WATER-PLANTAIN BUTTERCUP

Ranunculus occidentalis Nutt. in T. & G. — WESTERN BUTTERCUP

Ranunculus orthorhynchus Hook. — STRAIGHTBEAK BUTTERCUP

**Ranunculus repens* L. — CREEPING BUTTERCUP

Ranunculus uncinatus D. Don in G. Don — LITTLE BUTTERCUP

RHAMNACEAE

Rhamnus purshiana DC. — CASCARA

ROSACEAE

Amelanchier alnifolia (Nutt.) Nutt. — WESTERN SERVICEBERRY

Crataegus douglasii Lindl. — BLACK HAWTHORN

**Crataegus monogyna* Jacq. — ENGLISH HAWTHORN

Fragaria virginiana Duchesne — WILD STRAWBERRY

Geum macrophyllum Willd. var. *macrophyllum* — OREGON AVENS

Malus fusca (Raf.) Schneid. [*Pyrus fusca* Raf.] — WESTERN CRABAPPLE

Oemleria cerasiformis (H. & A.) Landon — INDIAN PLUM

Physocarpus capitatus (Pursh) Kuntze — PACIFIC NINEBARK

Potentilla gracilis Dougl. ex Hook. — SLENDER CINQUEFOIL

Rosa gymnocarpa Nutt. — BALDHIP ROSE

Rosa pisocarpa Gray — CLUSTER WILD ROSE

Rubus leucodermis Dougl. ex T. & G. — BLACKCAP

Rubus parviflorus Nutt. — THIMBLEBERRY

Rubus spectabilis Pursh — SALMONBERRY

Rubus ursinus C. & S. — PACIFIC BLACKBERRY

Sanguisorba occidentalis Nutt. — ANNUAL BURNET

Spiraea douglasii Hook. — DOUGLAS' SPIRAEA

RUBIACEAE

**Galium aparine* L. — CLEAVERS

Galium oreganum Britt. — OREGON BEDSTRAW

Galium trifidum L. — SMALL BEDSTRAW

Galium triflorum Michx. — FRAGRANT BEDSTRAW

SALICACEAE

Populus balsamifera L. ssp. *trichocarpa* (T. & G.) Brayshaw [*P. trichocarpa* T. & G.] — BLACK COTTONWOOD

Salix hookeriana Barratt ex Hook. [*S. piperi* Bebb] — HOOKER WILLOW

Salix lucida Muhl. ssp. *lasiandra* (Benth.) E. Murray [*S. lasiandra* Benth.] — PACIFIC WILLOW

Salix sitchensis Sanson ex Bong. — SITKA WILLOW

Walker Flat. Central meadow in June. Photo by Richard Halse.

Walker Flat. Wetland. Photo by Richard Halse.

SAXIFRAGACEAE
Chrysosplenium glechomifolium Nutt. [*C. glechomaefolium* Nutt.] — WESTERN GOLDEN-CARPET
Mitella caulescens Nutt. — LEAFY MITREWORT
Tiarella trifoliata L. var. *trifoliata* — TREFOIL FOAMFLOWER
Tolmeia menziesii (Pursh) T. & G. — PIG-A-BACK
SCROPHULARIACEAE
Collinsia grandiflora Lindl. — LARGE-FLOWERED BLUE-EYED MARY
**Digitalis purpurea* L. — FOXGLOVE
Mimulus guttatus DC. — YELLOW MONKEYFLOWER
Veronica americana (Raf.) Schwein. ex Benth. — AMERICAN BROOKLIME
Veronica peregrina L. — PURSLANE SPEEDWELL
Veronica serpyllifolia L. — THYME-LEAVED SPEEDWELL
URTICACEAE
Urtica dioica L. ssp. *gracilis* (Ait.) Selander — STINGING NETTLE
VIOLACEAE
Viola adunca Smith — EARLY BLUE VIOLET
Viola glabella Nutt. — STREAM VIOLET
Viola palustris L. — MARSH VIOLET
Viola sempervirens Greene — EVERGREEN VIOLET

Liliopsida (Monocots)
ARACEAE
Lysichiton americanum Hultén & St. John [*Lysichitum americanum* Hultén & St. John] — SKUNK CABBAGE
CYPERACEAE
Carex arcta Boott — NORTHERN CLUSTERED SEDGE
Carex hendersonii Bailey — HENDERSON'S SEDGE
Carex laeviculmis Meinsh. — SMOOTH-STEM SEDGE
Carex lenticularis Michx. var. *lipocarpa* (Holm) Standley [*C. lenticularis* Michx. var. *lenticularis*] — KELLOGG'S SEDGE
Carex obnupta Bailey — SLOUGH SEDGE
Carex ovalis Good [*C. leporina* L.] — HARE SEDGE
Carex pachystachya Cham. — THICKHEADED SEDGE
Carex stipata Muhl. — SAWBEAK SEDGE
Carex unilateralis Mack. — ONE-SIDED SEDGE
Carex utriculata Boott [*C. rostrata* Stokes misapplied] — BEAKED SEDGE
Eleocharis acicularis (L.) R. & S. — NEEDLE SPIKE-RUSH
Eleocharis ovata (Roth) R. & S. — OVOID SPIKE-RUSH
Scirpus microcarpus Presl — SMALL-FRUITED BULRUSH
IRIDACEAE
Iris tenax Dougl. — OREGON IRIS
Sisyrinchium angustifolium Mill. — BLUE-EYED GRASS
JUNCACEAE
Juncus acuminatus Michx. — TAPERED RUSH
Juncus bufonius L. — TOAD RUSH
Juncus covillei Piper — COVILLE'S RUSH
Juncus effusus L. — COMMON RUSH
Juncus ensifolius Wikstr. — DAGGER-LEAF RUSH
Juncus patens E. Meyer — SPREADING RUSH
Luzula comosa E. Meyer [*L. campestris* (L.) DC.] —FIELD WOOD-RUSH

Luzula divaricata Wats. — SPREADING WOODRUSH
Luzula parviflora (Ehrh.) Desv. — SMALL-FLOWERED WOODRUSH

LILIACEAE

Camassia leichtlinii (Baker) Wats. var. *suksdorfii* (Greenm.) Hitchc. — LEICHTLIN'S CAMAS
Lilium columbianum Hanson ex Baker — OREGON LILY
Maianthemum dilatatum (Wood) Nels. & Macbr. — BEADRUBY
Maianthemum stellatum (L.) Link [*Smilacina stellata* (L.) Desf.] — STAR-FLOWERED SOLOMON-PLUME
Prosartes hookeri Torr. [*Disporum hookeri* (Torr.) Nichols.] — HOOKER FAIRY-BELL
Prosartes smithii (Hook.) Utech, Shinwari & Kawano [*Disporum smithii* (Hook.) Piper] — SMITH FAIRY-BELL
Trillium ovatum Pursh — WESTERN WAKE-ROBIN
Veratrum californicum Durand var. *caudatum* (Heller) Hitchc. — CALIFORNIA FALSE HELLEBORE

ORCHIDACEAE

Calypso bulbosa (L.) Oakes — FAIRY-SLIPPER
Listera cordata (L.) R. Br. — HEART-LEAF LISTERA
Platanthera leucostachys Lindl. [*Habenaria dilatata* (Pursh) Hook. var. *leucostachys* (Lindl.) Ames] — WHITE BOG-ORCHID

POACEAE

Agrostis capillaris L. [*A. tenuis* Sibth.] — COLONIAL BENTGRASS
Agrostis scabra Willd. — WINTER BENTGRASS
Agrostis stolonifera L. [*A. alba* L.] — FIORIN
Aira caryophyllea L. — SILVER HAIRGRASS
Alopecurus geniculatus L. — WATER FOXTAIL
Arrhenatherum elatius (L.) Beauv. ex J. & C. Presl — TALL OATGRASS
Bromus sitchensis Trin. — ALASKA BROME
Bromus vulgaris (Hook.) Shear var. *vulgaris* — COLUMBIA BROME
Cinna latifolia (Trevir. ex Goepp.) Griseb. — WOODREED
Dactylis glomerata L. — ORCHARD-GRASS
Danthonia californica Boland — CALIFORNIA OATGRASS
Deschampsia elongata (Hook.) Munro ex. Benth. — SLENDER HAIRGRASS
Elymus glaucus Buckl. var. *glaucus* — BLUE WILDRYE
Festuca arundinacea Schreb. — TALL FESCUE
Festuca occidentalis Hook. — WESTERN FESCUE
Festuca pratensis Huds. — MEADOW FESCUE
Festuca rubra L. — RED FESCUE
Festuca subulata Trin. — BEARDED FESCUE
Glyceria elata (Nash) Jones — TALL MANNAGRASS
Glyceria leptostachya Buckl. — SLENDER-SPIKE MANNAGRASS
Holcus lanatus L. — VELVET-GRASS
Hordeum brachyantherum Nevski — MEADOW BARLEY
Lolium perenne L. — PERENNIAL RYEGRASS
Melica subulata (Griseb.) Scribn. — ALASKA ONIONGRASS
Phleum pratense L. — TIMOTHY
Pleuropogon refractus (Gray) Benth. — NODDING SEMAPHOREGRASS
Poa trivialis L. — ROUGHSTALK BLUEGRASS
Trisetum canescens Buckl. — TALL TRISETUM
Trisetum cernuum Trin. — NODDING TRISETUM
Vulpia myuros (L.) Gmel. var. *myuros* [*Festuca myuros* L.] — RAT-TAIL FESCUE

SPARGANIACEAE

Sparganium emersum Rehmann — SIMPLESTEM BUR-REED

TYPHACEAE

Typha latifolia L. — COMMON CAT-TAIL

Acknowledgements

Without the support of McMinnville Water and Light and CH2M HILL, Inc., this study would not have been possible. Special thanks are due Jack Nicholls and Rick Mishaga. We also are grateful to Kathy Merrifield for her generous identification of the bryophytes.

References

Bureau of Land Management. 1985. Distribution and status determination of *Sidalcea nelsoniana* Piper: a report to the Fish and Wildlife Service for status determination. Salem District BLM.

Chambers, K.L. and S. Sundberg. 1998. Oregon vascular plant checklist: Asteraceae. Oregon Flora Project, Oregon State University, Corvallis.

Christy, J.A., J.H. Lyford, and D.H. Wagner. 1982. Checklist of Oregon mosses. The Bryologist 85:22-36.

CH2M HILL, Inc. 1986, 1987, 1989, 1990b, 1991. Studies of *Sidalcea nelsoniana*. Prepared for City of McMinnville Water and Light Department.

CH2M HILL, Inc. 1990a. Coastal mountain wetlands in western Yamhill County: compilation of existing data. Prepared for City of McMinnville Water and Light Department.

CH2M HILL, Inc. 1992-1997, annually. Technical memorandum: *Sidalcea nelsoniana* monitoring. Prepared for City of McMinnville Water and Light Department.

Federal Register. 1993. Endangered and threatened wildlife and plants: determination of threatened status for the plant, "*Sidalcea nelsoniana*" (Nelson's checker-mallow). U.S. Fish and Wildlife Service. Final Rule. Federal Register 58(28):8235-8243.

Flora of North America Editorial Committee, eds. 1993. *Flora of North America*, Vol. 2, Oxford University Press, New York.

Glad, J.B., R. Mishaga, and R. R. Halse. 1987. Habitat characteristics of *Sidalcea nelsoniana* Piper (Malvaceae) at Walker Flat, Yamhill County, Oregon. Northwest Science 61:257-263.

Guerrant, E.O., Jr. 1997. Monitoring Nelson's checker-mallow (*Sidalcea nelsoniana*) at Walker Flat, Neverstill, and South McGuire: 1997. The Berry Botanic Garden. Prepared under a Challenge Cost-Share Agreement with the USDI Bureau of Land Management, Salem District, Oregon.

Hickman, J.C., ed. 1993. *The Jepson Manual*. University of California Press, Berkeley.

Hitchcock, C. L. and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle.

Oregon Department of Agriculture. 1989. State list of endangered and threatened plant species.

Stotler, R. and B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. The Bryologist 80:405-428.

Dr. Richard R. Halse has worked as a botanical consultant in Oregon, Washington and California. He is currently Curator of the OSU Herbarium and Instructor in the Department of Botany and Plant Pathology. Judith B. Glad, MSc, is a botanical consultant who has conducted qualitative and quantitative vegetation studies for a variety of clients throughout the western United States and Canada.

The *Eunanus* Monkey Flowers of Genus *Mimulus* (Scrophulariaceae) in Oregon

Wayland L. Ezell
2403 Pamo Court, Copperopolis, CA 95228

KEY WORDS: *Ecotypes,* Mimulus clivicola, Mimulus cusickii, Mimulus jepsonii, Mimulus nanus, *monkey flower, Scrophulariaceae*

*Abstract***.** In Oregon, four monkey flower species of the section *Eunanus* have been reported: *Mimulus nanus*, *M. cusickii*, *M. clivicola,* and *M. jepsonii*. *Mimulus nanus* is reproductively isolated from *M. cusickii*, even when they are sympatric. It exhibits ecotypic variation, with two ecotypes identified: typical *M. nanus* and a second form in lodgepole pine forests above 1220 m in the central and southern Cascades of Oregon. In the southern Oregon Cascades, *M. jepsonii* appears to intergrade

The genus *Mimulus* (Scrophulariaceae) includes seven polytypic and three to six monotypic sections, distributed primarily in western North American (Grant 1924; Pennell 1951). Monkey flowers are small shrubs (section *Diplacus*), or annual or perennial herbs. Of the 114 species listed by Grant (1924), 19 are included in the *Flora of the Pacific Northwest* (Hitchcock and Cronquist 1973). The second largest section, *Eunanus*, contains 20-plus annual species of desert, semi-desert, and montane habitats in the western United States, with four species reported from Oregon: *Mimulus nanus* Hooker and Arnott, *M. cusickii* (Greene) Piper, *M. clivicola* Greenman, and *M. jepsonii* Grant (Grant 1924; Pennell 1951). The first three are described in the *Flora of the Pacific Northwest*, but *M. jepsonii* is not included because it is limited to southern Oregon, below the 44th Parallel. *Mimulus nanus*, *M. cusickii*, and *M. jepsonii* also occur in California and are listed in *The Jepson Manual* (Thompson 1993).

In Oregon, herbaceous annual *Mimulus* species of other sections are distinguished from the *Eunanus* species and those of section *Oenoe*—*M. douglasii* (Bentham) Gray, *M. kelloggii* (Greene) Gray, and *M. tricolor* Lindley—by the following characteristics: pedicels usually longer than the leaves and yellow corollas that detach after withering (non-marcescent). In contrast, the *Eunanus* and *Oenoe* species have short pedicels and rose-pink to reddish-purple corollas that remain attached after withering (marcescent corollas). *Oenoe* species differ in having the pedicel attached obliquely (asymmetrical) to the capsule, the calyx base swollen on one side (gibbous), and the slender corolla tube mostly twice as long as the calyx (Grant 1924).

Mimulus clivicola is a distinct species known only from the Snake River Canyon (Wallowa and Baker counties in eastern Oregon, and Kootenai, Latah, and Idaho counties in Idaho). It is distinguished from the other three *Eunanus* species by its slightly toothed (serrate) leaves, long pedicels (up to 10 mm), and expanded calyx with a wedge-shaped (cuneate) base when the capsule is mature.

Mimulus cusickii has less morphological variation than *M. nanus*, with a more restricted geographical and ecological distribution. It grows in sandy or rocky soil in exposed areas across the interior plateau from central Oregon to western Idaho, with limited populations in Modoc County of northern California and Washoe County in northwestern Nevada. In Oregon, *M. cusickii* is found in Baker, Crook, Deschutes, Gilliam, Grant, Harney, Jefferson, Josephine, Klamath, Lake, Malheur, and Wasco counties. Unlike *M. nanus,* it does not occur at higher elevations in the Blue Mountains and Wallowa Mountains of northeastern Oregon. In Deschutes County, *M. cusickii* and *M. nanus* occur sympatrically in sandy or rocky, often pumice, soil in areas of western juniper-sagebrush (*Juniperus occidentalis*/*Artemisia tridentata*) scrub to ponderosa pine (*Pinus ponderosa*) forests on the east slopes of the Cascade Mountains.

Mimulus nanus is widely distributed in the northwestern United States and has considerable ecological and morphological variation. The form similar to the nomenclatural type occurs in Oregon, southern Washington, Idaho, southwestern Montana, Yellowstone National Park, northern Nevada, and northern California. In southern Oregon, northern California, and northwest-

Typical *Mimulus nanus* flower. Central Oregon. Photo by Wayland Ezell.

ern Nevada, plants generally identified as *M. nanus* exhibit floral characters which differ from the nomenclatural type. Habitats in Oregon range from open sites in ponderosa pine forests, western juniper-sagebrush associations, and desert sagebrush of central and eastern Oregon, to higher elevations in the Blue, Wallowa, and Steens Mountains, into the open habitats of Idaho and adjacent states. In Oregon, it occurs in Baker, Crook, Deschutes, Gilliam, Grant, Harney, Jackson, Jefferson, Josephine, Klamath, Lake, Malheur, Morrow, Sherman, Union, Wallowa, and Wheeler counties.

A form grows in lodgepole pine (*Pinus contorta*) forests between 1220-1830 m elevation on the eastern slopes of the Cascade Mountains from Deschutes County, south to Klamath and Lake counties of southern Oregon. Although usually identified as *M. nanus*, it is distinguished from the nomenclatural type of *M. nanus* by its reddish-purple corolla tube and lobes and the absence of dark lateral patches in the throat. Typical *M. nanus* has a corolla with a yellow tube, reddish-purple lobes, and two dark-purple lateral patches in the throat. In Deschutes County, at the limited zones of contact of typical *M. nanus* and the Cascade form, morphologically intermediate forms, and typical parental types, occur sympatrically, suggesting gene flow between the two. Putative hybrids have flowers with intermediate traits: a reddish-purple corolla tube with two dark-purple lateral throat patches, or a yellow corolla tube with no dark patches in the throat.

Based on ecological and morphological differences between the Cascade form in lodgepole pine habitats and typical *M. nanus*, and the possible interfertility between the two, it is hypothesized that they are ecotypes, as defined by Clausen and Hiesey (1958) and Clausen *et al*. (1940, 1945). In this paper, the term ecotype is used in the sense of Clausen *et al.* (1945, p. 63) who define ecotypes as:

> *Species that occupy a series of contrasting environments develop genetically and physiologically distinct ecologic races, ecotypes, which are suited to these environments. Ecotypes of one species have the same internal balance, for there is no genetic obstacle to a free interchange of their genes when they meet and hybridize.*

Mimulus jepsonii ranges from Nevada County, California, in the Sierra Nevada to the Cascade range of California and southern Oregon, as far north as Davis Lake (Klamath County) and Douglas County, Oregon (Grant 1924; Thompson 1993). Plants resembling the nomenclatural type center in northern California and southern Oregon at elevations of 1830-2440 m. They exhibit little morphological variation and are similar to typical *M. nanus*, distinguished by a reduction in plant height (up to 8 cm tall vs. 14 cm), reduced lengths of the calyx (2-5 mm vs. 6-9 mm), corolla (9-14 mm vs. 15-25 mm), and capsule (4-6 mm vs. 6-10 mm). Also, the upper pair of anthers are located at the same level as the stigma (a condition favoring self-pollination), whereas in *M. nanus* the upper anthers are at least 1-2 mm below the stigma. Other than a reduced length, corollas of *M. nanus* and *M. jepsonii* are alike in their strongly bilabiate form and pigmentation: yellow tube and reddish-purple lobes with two dark-purple lateral patches in the throat. The overall reduced size of high-elevation plants may be due to the shorter growing season, which favors the selection of genes for rapid maturation. A shorter growing season also could contribute to reduced plant dimensions, because more energy is directed to flower maturation and capsule formation than to vegetative growth. This potential for facultative self-pollination in specimens above 1830 m is of possible adaptive significance because of the limited numbers of insect pollinators at higher elevations.

Typical *M. nanus* generally occurs below 1525 m. However, at elevations between 1220-1830 m in the southern Cascade Mountains of Oregon, forms are found which are morphologically similar to both *M. jepsonii* and typical *M. nanus*, but are intermediate in the lengths of the calyces, corollas, and capsules, with this variation appearing to be clinal. From Lassen Volcanic National Park northward, *M. jepsonii* appears to intergrade with typical *M. nanus*, and in southern Oregon, possibly also with the Cascade form of *M. nanus*. The lower-elevation (below 1830 m) specimens of *M. jepsonii* are more similar to typical *M. nanus* in their breeding system, with the upper pair of anthers 1-2 mm below

Table 1. Descriptions and locations of study sites for *M. nanus* and *M. cusickii* in central Oregon.

Site No.	Description	Location	Species	Elev. (m)
001	Transitional zone between ponderosa pine and western juniper	5.5 km E of Sisters, Deschutes Co., S of US Highway 126	*M. nanus* (typical)	946
003	Juniper-sagebrush habitat	10.5 km E of Redmond, S of US Highway 126	*M. cusickii*	915
092	Ponderosa pine forest fringing eastern base of Cascade Mountains	1.5 km W of Sisters, Deschutes Co., N of US Highway 20	*M. cusickii* *M. nanus* (typical)	976
108	Lodgepole pine forest	0.8 km S of entrance to W Davis Lake public campsite, Klamath Co.	*M. nanus* (Cascade form)	1342
130	Lodgepole pine forest	35.4 km S of Bend, Deschutes Co., NE corner of US Highway 97 & Paulina-East Lake Rd.	*M. cusickii* *M. nanus* (Cascade form)	1281

the stigma. These morphological similarities between *M. jepsonii* and typical *M. nanus,* and the presence of possible intergrades in the field, suggest gene flow between the two.

To test the hypothesis that the Cascade form is an ecotype and can be classified as a subspecies of *M. nanus*, I studied the genetics and ecology of *M. nanus* and *M. cusickii* in central Oregon at the sites listed in Table 1. Seven populations were selected from five sites in Deschutes, Crook, and Klamath counties (Ezell 1971). All five sites were exposed, open areas with loose, sandy soil.

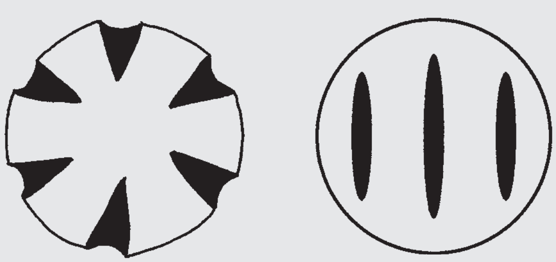
Chromosome Counts

The taxa of the seven field populations (Table 1) had a gametic chromosome number of n=8 (Ezell 1971, 1975). This agrees with the first published count in section *Eunanus, M. brevipes* (Mukherjee and Vickery 1962) and the counts for *Eunanus* species by Thompson (1993). Ezell (1972) reported tetraploidy (n=16) in *M. bigelovii* var. *bigelovii*, an annual species similar to *M. cusickii* native to the deserts of southern California and adjacent Nevada. Closely related species usually have the same number of chromosomes, or in the case of polyploidy, have the same base number. For example, species of the annual herbaceous sections *Eunanus* and *Oenoe* have a base number of 8; diploids (2X) are 2N=16, with the tetraploid (4X) *M. bigelovii* being 2N=32. The shrubby species in section *Diplacus*, on the other hand, are diploids (2N=20), with a base number of 10.

Pollen Morphology

Mimulus nanus and *M. cusickii* pollen grains are spherical with three to eight equatorial furrows (colpi), a trait defined as stephanocolpate by Kapp (1969). Ezell (1979) reported the pollen of these species to be three-seven stephanocolpate and four-eight stephanocolpate, respectively. Argue (1980) described the pollen of these two species, and 20 other *Eunanus* species, as five-seven stephanocolpate, with *M. densus* being four-eight stephanocolpate. In *M. nanus*, 66-82 percent of the grains have five colpi, whereas 56-72 percent are six-colpate in *M. cusickii* (Ezell 1971). It is assumed this difference is genetic and can be used to distinguish between the two species. Ezell (1979) hypothesized that a large number of apertures could facilitate rapid pollen tube growth, leading to rapid fertilization in the arid desert conditions to which these taxa are adapted. Species of a second major annual section (*Oenoe*) also occupy xeric habitats, and Argue (1980) also reported five-seven stephanocolpate pollen for these species.

A colpus (plural: colpi) is a furrow (aperture) more than twice as long as broad in the wall of a pollen grain. Stephanocolpate pollen have a variable number of equatorial furrows per pollen grain.



Left, polar view of a 6-stephanocolpate pollen grain; right, equatorial view of a stephanocolpate pollen grain showing three colpi. Illustration by Wayland Ezell.

Site 092: Ponderosa pine habitat near Sisters, Oregon. Photo by William Chilcote.

Greenhouse Hybridizations

Intraspecific crosses in typical *M. nanus* (sites 001, 092) and *M. cusickii* (sites 003, 092, 130) produced normal or near-normal seed set, similar to natural seed set in field populations. Greenhouse crosses between the two *M. nanus* ecotypes produced seeds, supporting field observations of possible gene flow when the two occur sympatrically. I concluded that these two forms are genetically compatible, but in nature, they usually are isolated by spatial or ecological factors. This supports their status as ecotypes and their classification as subspecies.

Greenhouse cultures of typical *M. nanus* (site 001), the Cascade ecotype (site 108), and *M. cusickii* (site 003), when self-pollinated by hand in the greenhouse, produced capsules with a mean seed set per capsule similar to greenhouse intrapopulation mean seed sets. These plants have the potential to be self-compatible, but cross-pollination is the normal mode because the flowers structurally are adapted for outcrossing. The receptive stigmatic surface is 1-2 mm above the upper pair of anthers, and the bilobed stigmas close when physically contacted, thereby avoiding self-pollination by insect visitors. Withered intact flowers (not hand-pollinated), randomly collected in the greenhouse, possessed dried and shriveled ovaries and ovules, indicating that self-pollination normally does not occur.

Although evidence corroborates the idea that these species are insect-pollinated facultative outcrossers, the specific pollinators were not identified by field observations. The only insects observed visiting the seven field populations were syrphid flies (Diptera: Syrphidae), which would be poor pollinators due to their lack of appreciable external hairs and bristles. Samples of these flies collected after visiting *Mimulus* flowers carried no pollen.

Environmental Influence on Plant Height and Capsule Length

Plant height is influenced by environmental conditions, with plants being depauperate under xeric conditions and taller with more nodes, branches, and flowers during periods of greater rainfall. Greenhouse cultures of these taxa, when watered on a regular basis, grew to more than three to four times the height in field populations, with numerous flowers per plant. Under dry field conditions, de-pauperate forms only produce one or two flowers. Therefore, the potential for plant height is an open genetic program, heavily influenced by the environment.

Mean capsule lengths within populations of *M. nanus* and *M. cusickii* (collected at different times over three years) were constant for each species. The mean length of capsules from greenhouse cultures was similar to field populations, indicating the potential for capsule length is a closed genetic program, with little or no environmental influence.

Mimulus cusickii flower. Central Oregon. Photo by Wayland Ezell.

Summary of Ecotypic and Taxonomic Relationships

Mimulus cusickii is a genetically distinct species in central Oregon, and based on field observations and herbarium studies, is a distinct species throughout its range. Greenhouse hybridization results support field observations of no gene exchange between *M. nanus* and *M. cusickii* in central Oregon where they are sympatric. It is distinguished from *M. nanus* by its mephitic (skunk) odor and distinctive flowers. Its rose-pink to reddish corollas are slightly bilabiate with nearly equal lobes, somewhat rotate, and the upper and lower lips are nearly equal, whereas the reddish-purple corollas of *M. nanus*

Key to the Species and Ecotypes of the *Eunanus* Monkey Flowers in Oregon

A. Leaf margins finely toothed (serrulate); pedicels 2-10 mm long; calyx base wedge-shaped (cuneate) when capsule matures; upper .... anther pair usually included in corolla throat; northeastern Oregon and adjacent Idaho
1. ***Mimulus clivicola***

A. Leaf margins not toothed (entire); pedicels 0.5-4 mm long; calyx base rounded when capsule matures; upper anther pair usually .... exserted from corolla throat

- **B.** Corolla not strongly bilabiate, somewhat rotate, 18-35 mm long, lobes rose-pink to reddish-purple, nearly equal; pedicels 1-4 mm long; leaf tips acute to acuminate; herbage with mephitic odor; 900-1300 m elev. in central and eastern Oregon .... 2. ***Mimulus cusickii***
- **B.** Corolla strongly bilabiate, 9-25 mm long, lobes reddish-purple, upper lip erect and longer than lower lip; pedicels 0.5-2 mm long; leaf tips obtuse; herbage lacking mephitic odor
  - **C.** Leaves broadly elliptic to obovate or oblanceolate, 2-15 mm broad, 5-30 mm long; calyx 4-9 mm long; corolla 12-25 mm long, funnelform; upper anther pair 1-2 mm below stigma; capsule 5-10 mm long
    - **D.** Leaves elliptic to oblanceolate; corolla tube yellow, two dark-purple lateral patches in throat; calyx 6-9 mm long; capsule 6-10 mm long, slightly if at all exserted from calyx; widespread at 900-1830 m elev. in central and eastern Oregon .... **3. Typical *Mimulus nanus***
    - **D.** Leaves elliptic to obovate; corolla tube reddish-purple, no dark-purple lateral patches in throat; calyx 4-7 mm long; capsule 5-8 mm long, exserted from calyx; 1220-1830 m elev. in lodgepole pine habitats of Oregon Cascades (Douglas, Klamath & Lake counties) .... **4. Cascade ecotype of *Mimulus nanus***
  - **C.** Leaves narrowly elliptic-oblanceolate to linear-oblong, 1-6 mm broad, 4-18 mm long; calyx 2-5 mm long; corolla

Flower of Cascade ecotype of *Mimulus nanus*. Central Oregon. Photo by Wayland Ezell.

are strongly bilabiate, with the upper lip erect and usually longer than the lower lip.

There also are phenological differences between the two species. In field populations, seeds of typical *M. nanus* germinate 2-4 weeks earlier, and their growing season ends 4-6 weeks earlier than *M. cusickii*. Plants of the latter have a growing season of 3-4 months (June through September), compared to 2-3 months (May through July) for *M. nanus.* Despite a brief overlap in anthesis within sympatric populations, there are no morphological indications of hybridization. Absence of hybridization is also supported by greenhouse crossing studies.

Results obtained from morphological data, field observations and greenhouse hybridizations support the hypothesis that the Cascade form in the lodgepole pine forest is an ecotype of *M. nanus*. Greenhouse hybridization results support the field observations of possible gene flow at their zones of overlap in Deschutes County; therefore, it can be classified as a subspecies of *M. nanus*.

Morhological and ecological data from a study of herbarium specimens and field collections, indicate that *M. jepsonii* hybridizes with *M. nanus* along their zones of overlap in the southern Oregon Cascades, supporting the hypothesis of it also being an ecotype of *M. nanus*. If genetic studies demonstrate actual gene flow between the two, it could be concluded that *M. jepsonii* is an ecotype of *M. nanus* and then classified as a subspecies of *M. nanus*.

Acknowledgements

This paper is based on a doctoral dissertation submitted to the Department of Botany and Plant Pathology, Oregon State University. I wish to acknowledge and thank Dr. Kenton L. Chambers for his guidance during this investigation and his continued friendship. I thank the curators and directors of these herbaria for loans (BH, CAS, CU, DS, GH, ILL, JEPS, MO, NY, PENN, PH, POM, RM, RSA, UC, US, WS, WTU) and the opportunity to visit their herbaria (BM, K, MIN, OKL, OKLA, OSC, POM, RSA, UC, US). These herbarium abbreviations are based on those in the *Index Herbariorum* (Holmgren *et al*. 1990). Field research was supported by two Grants-in-Aid of Research from the Society of the Sigma Xi. Travel to the U.S. National Herbarium was funded by a St. Cloud State University Faculty Research Grant. Aaron Liston, Cindy Roché, and Linda Vorobik reviewed the manuscript and provided critical comments.

References

Argue, C.L. 1980. Pollen morphology in the genus *Mimulus* (Scrophulariaceae) and its taxonomic significance. American Journal of Botany 67:68-87.

Clausen, J. and W.M. Hiesey. 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. Carnegie Institute of Washington Publication 615.

Clausen, J., D.D. Keck, and W.M. Hiesey. 1940. Experimental studies on the nature of species. I. Effects of varied environments on North American plants. Carnegie Institute of Washington Publication 520.

Clausen, J., D.D. Keck, and W.M. Hiesey. 1945. Experimental studies on the nature of species. II. Plant evolution through amphiploidy and autoploidy with examples from Madiinae. Carnegie Institute of Washington Publication 56.

Ezell, W.L. 1971. Biosystematics of the *Mimulus nanus* complex in Oregon. PhD thesis, Oregon State University, Corvallis.

Ezell, W.L. 1972. In IOPB chromosome number reports XXXVIII. Taxon 21:681.

Ezell, W.L. 1975. Ecotypic variation in the *Mimulus nanus* complex. Abstract, page 53 in Botanical Society of America Miscellaneous Publication.

Ezell, W.L. 1979. Adaptive significance of aperture number in *Mimulus* (Scrophulariaceae) pollen grains. Abstract, page 1 in Minnesota Academy of Science Miscellaneous Publication.

Grant, A. L. 1924. A monograph of the genus *Mimulus.* Annals of the Missouri Botanical Garden 11:99-389.

Hitchcock, C. L. and A. Cronquist. 1973. *Flora of the Pacific Northwest.* University of Washington Press, Seattle.

Holmgren, P.K., N.H. Holmgren, and L.C. Barnett. 1990. *Index Herbariorum, Part I: the Herbaria of the World*, eighth edition. New York Botanical Garden, Bronx, NY.

Kapp, R.O. 1969. Pollen and spores. W.C. Brown, Dubuque, IA.

Mukherjee, B.B. and R.K. Vickery, Jr. 1962. In Documented chromosome numbers in plants. Madroño 16:267.

Pennell, F.W. 1951. *Mimulus*. Pages 688-731 in L. Abrams, ed. Illustrated Flora of the Pacific states, volume 3. Stanford University Press, Stanford, CA.

Thompson, D.M. 1993. *Mimulus*. Pp. 1037-1046 in J.C. Hickman, ed., *The Jepson Manual.* University of California Press, Berkeley.

Wayland L. Ezell is Professor Emeritus, Department of Biological Sciences, St. Cloud State University (SCSU), Minnesota, where he was professor of Botany and Curator of the SCSU Herbarium before his 1999 retirement. He earned a PhD in Botany from Oregon State University under the direction of Ken Chambers.

Non-morphological Evidence in Biosystematics: Kenton Chambers and the Annual Species of *Microseris*

Konrad Bachmann
Institut für Pflanzengenetik und Kulturpflanzenforschung
IPK, D-06466 Gatersleben, Germany

KEY WORDS: *biosystematics,* Microseris*, species recognition, taxonomic methods.*

Abstract. In the first half of the 20th century, biosystematics introduced non-morphological methods to aid in the recognition of species. Although biosystematists acknowledged that there is no generally applicable uniform species concept, they were able to assemble explicit criteria for species recognition based on population biology. This started a succession of new techniques in taxonomy that occasionally has been criticized as contributing less than expected and mainly at lower taxonomic levels. Chambers's 1955 monograph on the annual species of *Microseris* (Asteraceae) is evaluated as a classical biosystematic technique in the light of a great deal of data obtained since then by newer techniques. It is shown that methods such as common garden experiments, the analysis of breeding behavior, ploidy determinations and studies of hybrid sterility were essential to achieving an urgently needed rational and stable basis for taxonomy. Biosystematic methods became indispensable, profitable at a level where they were most needed, and eventually prepared the way for continued restructuring of taxonomy by the comparative analysis of genomes.

There is a wide-spread belief among plant systematists that new methods emerge at fifteen year intervals, each one presented as offering the definitive set of characters for phylogenetic analysis, only to be superseded in due time by the next, even more modern method. Wagenitz (1996) recently extended this view to include aspects of molecular systematics. Since a continuous search for better methods is an essential part of science, the criticism implied in this interpretation concerns the perceived discrepancy between the excessive claims made for each new approach and the modest degree of real progress, especially relative to the solid and continuous contributions from morphology.

This short-coming appeared not to apply to molecular taxonomy. With access to the nucleotide sequence of the genome in nuclei and organelles, we had reached the ultimate source of phylogenetically relevant evidence preserved in living organisms in a form ready-made for computer analysis. At first, phylogenetic reconstruction finally seemed to have reached the status of a technical routine procedure. Since then we have uncovered formidable problems with the phylogenetic analysis from molecular data: reticulate evolution at all levels from organisms to single genes, genetic redundancy (Pickett and Meeks-Wagner 1995) and its bearing on the problem of homology, and the eventual disappearance of the phylogenetic signal in random mutational noise. Encountering these problems was a sobering experience, but the cause was not the molecular data. These underlying problems of phylogenetic reconstruction were exposed when sufficiently informative data became available. Now we realize how little phylogenetically relevant information in the genome is revealed by plant morphology and that morphological data can be deceptive for more complex reasons than adaptive convergence. Under the circumstances, it is remarkable how far classical taxonomy has come towards reconstructing a natural system.

However, non-morphological characters contributed significantly to plant taxonomy long before the advent of molecular methods. These approaches are referred to as "experimental taxonomy" or "biosystematics." As the major development in plant taxonomy between 1920 and 1950, these experimental methods brought no revolutionary revision of general taxonomic theory or practice, primarily since the new approach was relevant mainly at the level of species and contributed virtually nothing to higher-level taxonomy (Hagen 1983). However, because the great malaise of taxonomy at that time was at the level of species, the beneficial effect of biosystematic methods was spectacular and lasting (Chambers 1995).

With his PhD thesis, *A Biosystematic Study of the Annual Species of Microseris*, Kenton L. Chambers (1955) contributed a classic paper of the "glory days" of biosystematics. Since that time, *Microseris* has been examined with each new research method (Table 1) and nearly every aspect of Chambers's work has been repeated and verified. *Microseris* has been the topic of another eight PhD theses (Sneddon 1977, Mauthe 1984, Zentgraf 1986, Van Heusden 1990, Vlot 1993, Battjes 1994, Van Houten 1994, Roelofs 1996).

Few PhD theses have been examined so closely. This intensive testing has revealed such a flawless application of the best methods available at the time that I can use Chambers's 1955 monograph as representative of the achievements and limitations of classical biosystematics without having to make allowance for human error. I emphasize this because methods available in the 1950s did not guarantee correct results when mechanically applied. Some monographs from that period reached wrong conclusions by using the new methods for evidence to support instinctive assessments of relationships, rather than reserving taxonomic instinct to resolve problems left after the critical application of experimental methods.

Table 1. New methodology by which Chambers (1955) thesis was tested.

Technique	Publication
Nuclear DNA in relation to chromosome size	Price and Bachmann 1975
Nuclear DNA in relation to mitotic cycle time	Price and Bachmann 1976
Repetitive DNA	Bachmann and Price 1977
Phenotype	Bachmann *et al.* 1979
Ecological distribution	Price *et al.* 1981
Local dispersal mechanisms	Hobbs 1985
Long distance distribution	Chambers 1963
Isozymes	Irmler *et al.* 1982
Chemical systematics	Harborne 1977
Chromosome banding	Oud *et al.* 1988
Pollen ultrastructure	Feuer and Tomb 1977
Ultrastructure of chromatin	Nagl and Bachmann 1980
Phenotypic plasticity	Battjes and Bachmann 1994
Quantitative analysis of morphological variation	Bachmann and Battjes 1994
Molecular systematics	Wallace and Jansen 1990 Micro-
satellites	Van Houten *et al.* 1991
Restriction fragment length analysis and sequence evolution	Van Houten *et al.* 1993
Marker-assisted quantitative genetics	Gailing *et al.* 1999

Despite the essential contribution of experimental methods to successful analyses, intuitive assessment of morphological similarity and its taxonomic significance still played an important role in the biosystematics of the 1950s. Spotting the right characters and interpreting them properly on insufficient evidence has been the genius of great taxonomists. Kenton Chambers has this gift to perfection. As much as we admire the ability to intuitively recognize key factors amongst a bewildering variability, our efforts should aim to minimize the need for a special personal touch, striving to make taxonomy an objective, generally applicable, technical procedure. My aim here is to examine how the objective techniques of classical biosystematics reduced the need for intelligent guesses and where conjecture was still required. Using a specific case greatly facilitates this examination, but requires some introduction to the organisms under investigation.

The Background: 1769 to 1900

Table 2 lists the currently valid names of the species of *Microseris*. Most of the species are endemic to western North America, and North America is the home of their nearest relatives in the genera *Nothocalais* and *Agoseris* and the related genera *Stephanomeria*, *Krigia*, *Pyrrhopappus* and *Phalacroseris* (Jansen *et al.* 1991). By a quirk of history, the first species of the genus was discovered by Joseph Banks and D.C. Solander in New Zealand in 1769 during the first voyage of Captain Cook, and the second species of the genus was collected by Carlos Bertero in 1828 in Chile. In the same decade, the first specimens were collected in North America by David Douglas. The name *Microseris pygmaea*, given to the Chilean species by David Don (1832), has priority for the species and the genus. Joseph Dalton Hooker showed in 1853 that the plants from Australia and New Zealand were congeneric with the Chilean *Microseris* (Hooker 1853). Schultz-Bipontinus (1866) transferred the North American species of *Calais*, *Uropappus*, *Scorzonella,* and *Apargidium* to *Microseris*. This very brief outline of a very complex nomenclatorial history covers two great phases of plant taxonomy: 1) exploration, discovery, and description, and 2) sorting and ordering the material from all across the world and proposing a natural system.

By the end of the nineteenth century, the great outlines of the system were settled, and the daily routine of taxonomists turned to the innumerable details that had to be checked, adjusted and filled in. It is this phase in which some of the genera and subgenera in and around *Microseris* were united, separated, shifted, and reunited. These changes depend more on alternative interpretations of the same morphological data than on new data or new theories. For convenience, I have listed the species in Table 2 in seven groups that have been variously recognized as genera, subgenera or sections. In *A Manual of Flowering Plants of California* (Jepson 1957), we find group (1) under the genus name *Scorzonella* Nutt., and *M. borealis* (group 2) several pages away under the genus name *Apargidium* Torrey & Gray. *Uropappus lindleyi* (group 6) and *Stebbinsoseris* Chamb. (group 7) are valid names today. Their story will be examined below. In addition to the species listed in Table 2, the position of species now in genus *Nothocalais* relative to *Microseris* (*Scorzonella*) and *Agoseris* has been

Table 2. Valid names of *Microseris* and related species examined in this study.

(1) Diploid perennials, mostly outcrossing
M. howellii Gray
M. laciniata (Hook.) Sch-Bip.
M. nutans (Hook.) Sch.-Bip.
M. paludosa (Greene) Howell
M. sylvatica (Benth.) Sch.-Bip.

(2) Diploid annual, morphologically distinct (pappus)
M. borealis (Bong.) Sch.-Bip.

(3) Tetraploid perennials of Australia and New Zealand
M. scapigera (Sol. ex A. Cunningham) Sch.-Bip. including
M. lanceolata (Walp.) Sch.-Bip.
(ancestral annual x perennial similar to *M. borealis*)

(4) Diploid annuals, mostly autogamous
M. douglasii (DC.) Sch.-Bip.
M. elegans Greene ex Gray
M. bigelovii (Gray) Sch.-Bip.
M. pygmaea D. Don. (only Chilean species of *Microseris*)

(5) Tetraploid annuals of *Microseris*
M. acuminata Greene (extinct N.A. annual x *M. douglasii*)
M. campestris Greene (extinct N.A. annual x *M. elegans*)

(6) Diploid annual, morphologically distinct
Uropappus lindleyi (DC.) Nutt.

(7) Tetraploid annuals involving *U. lindleyi*
Stebbinsoseris decipiens (Chamb.) Chamb.
(*M. bigelovii* x *U. lindleyi*)
Stebbinsoseris heterocarpa (Nutt.) Chamb.
(*M. douglasii* x *U. lindleyi*)

TERMINOLOGY

apomorphic: derived from and differing from an ancestral condition, important for determining relationships in cladistic analyses

biosystematics: experimental taxonomy based on the study of evolution and biological information at the population level, such as genetic variability, hybridization, breeding strategies, competition, and local adaptions

clade: a branch of a cladogram, representing a monophyletic group of taxa sharing a closer common ancestry with one another than with members of other branches

cladogram: a branching diagram representing the relationships between characters from which phylogenetic inferences can be made

chloroplast genome: genetic code contained within the chloroplasts, significant as maternally inherited, rather than recombined during sexual reproduction

heterozygous: having different alleles at corresponding loci on a chromosome pair

homology: structurally similar charcteristics that share an evolutionary differentiation from the same or a corresponding part of a remote ancestor

homozygous: having identical alleles at corresponding loci on a chromosome pair

ITS internal transcribed spacer of nuclear genes for ribosomal RNA: sequence of genetic code used in taxonomic work to interpret evolutionary relationships among taxa

monomorphic: having but a single form, structural pattern, or genotype

monophyletic: derived from the same ancestral taxon

parsimony: economy in the use of means to an end; *especially* economy of explanation in conformity with Occam's razor, a philosophical rule that the simplest of competing theories be preferred to the more complex

phylogenetic: based on natural evolutionary relationships

plesiomorphic: ancestral or evolutionarily primitive state of a character

synapomorphic: common possesion of a derived characters by two or more taxa, considered in cladistic studies to be evidence of relationship

tetraploid: a polypoid having four sets of homologous chromosomes

a point of discussion (Chambers 1955).

Differences among taxonomists were not limited to the sober business of shuffling groups and weighing characters in order to see which arrangement would be the most convenient. Especially when it came to the delimitation of species, a tendency for "splitting" or "lumping" also reflected deep-seated differences of opinion and the absence of a theoretical basis on which to resolve these by objective criteria. When experimental systematics supplied such criteria, it led to a dramatic reduction in the number of accepted taxa, and further studies have amply supported the decision to recognize the fewer, more inclusive units as biological species. What were the criteria, what was the evidence, and how was it interpreted?

Species Recognition by a Biosystematist

Recently I have discussed the never-ending attempts to define a generally acceptable species concept in taxonomy, and have recommended to do away with the mandatory recognition of species as basic units in taxonomy (Bachmann 1998). The idea would have been unthinkable in 1955, and since the technical means for an alternative approach were unavailable at the time, it would have been useless. However, the problem of delimitating species was recognized more clearly and soberly in 1955 than ten years later or, possibly, today. Chambers (1955, p. 221) discusses the question of species recognition in detail, and begins his discussion with the remarkable statement,

> *An important axiom in taxonomy is that there are many different kinds of species ... It has been suggested by many that taxonomy, without exact definitions of such basic terms as 'species', cannot claim the distinction of a science. Yet, despite many attempts, no single criterion, nor any one generalization, has succeeded in defining species wherever they occur in the vast complexity of organic nature.*

What a graduate student calls an "axiom" in his thesis must be accepted wisdom of the day. Since then, if not the practice of taxonomy, certainly the theory of the field has regressed rather than advanced. Even if modern discussions of the species problem (Hull 1997) eventually come to the conclusion which Chambers already cited as an axiom in 1955, the search for the general and universal species concept has not been slowed by the realization that no such thing exists. Faced with the practical task of recognizing species and of accepting or rejecting previous species recognitions, a taxonomist needs some objective criteria. Chambers considers this a problem "of determining what kind or kinds of species occur in the particular group of organisms under investigation" (Chambers 1955, p. 222). For him, species are the "significant evolutionary units," and his practical guideline is the "species-standard" method of Rollins (1952).

In order to appreciate the task faced by Chambers, we have to reconstruct the starting condition. Chambers assumed that he had identified what we now would call a monophyletic group of plants. The plants which he selected for study occur in local populations in isolated patches of suitable soil, climate, and vegetation (Chambers 1955, p. 263); some, for instance, around vernal pools or on serpentine outcrops. Variation within and between populations is not continuous: a population usually consists of several distinct "biotypes". The neutral word "biotype" is significant. The fact that several biotypes, undoubtedly even several species, can exist in mixed populations, suggests that there is no obvious ecological differentiation among the biotypes (or species), and Chambers decidedly does not succumb to the opinion that recognizably different "types" within a species must of necessity be the result of local selection. This was, at the time, becoming the fashionable "pan-selectionist" hypothesis (Gould 1982). Occasionally, identical or very similar biotypes are found in several populations, and usually biotypes (of a species) within a population are more similar to each other than to biotypes from other populations. There is hardly any character that does not vary among biotypes, but most characters seem to be randomly associated across the entire distribution range (Bachmann *et al*. 1984; Bachmann and Battjes 1994) and sometimes within populations

(Chambers 1955, p. 266-267). In addition, most plant characters are very sensitive to environmental influence. Before all of this was sought out, the task of recognizing "significant evolutionary units" in this highly but very irritatingly structured pattern of variation must have seemed daunting.

The classical morphological approach in dealing with this situation would have been a "survey of the whole range of morphological variation and the recognition of 'forms' or modes of variation within this range" (Chambers 1955, p. 222). As stated above, biosystematic methods have not replaced morphological analysis; however, the limitations of such an analysis without additional information are very obvious in the case of the annual *Microseris*. Populations have characters, as have biotypes, and there are some striking individual characters that are widely distributed and easily recognized, even when they are associated with different characters in different populations. The numerous names proposed for annual *Microseris* by Greene (1905) recognize this level of variation without understanding its biological basis. On morphological grounds, the ultimate recognizable "form" in the annual *Microseris* would often have been a homozygous genotype.

In contrast, biosystematic treatment starts with an analytical phase in which individual plants in local populations are the units that are studied. Four typically biosystematic approaches contributed significantly to the success of this analysis: 1) raising the plants in a common (favorable) environment, 2) analyzing the breeding behavior of the plants, 3) counting chromosomes and determining the ploidy of the plants, and 4) analyzing fertility of artificial hybrids and chromosome pairing during their meiosis.

Genetic vs. Plastic Variation

Experimental systematics had started with an ecological approach in which plants from various populations were transplanted to the ecologically different sites of other populations (Hall and Clements 1923, Turesson 1923, Clausen *et al.* 1948). A central result of this line of investigation was the clear differentiation of genetically determined adaptation (ecotypic variation) and individual local responses to the environment (phenotypic plasticity). Such reciprocal experiments are too expensive and time consuming to become routine. What remained of them in biosystematic practice was the comparison of plants from different populations under common garden or greenhouse conditions with the aim of minimizing the influence of plastic responses.

These experiments have documented the high degree of plasticity of most characters of the annual species of *Microseris* and have shown that many (most?) plants in nature are depauperate compared to a genetic optimum morphology attained under favorable conditions (Chambers 1955, p. 265, Bachmann and Battjes 1994). Characters of fruit (achene) morphology are the least plastic in *Microseris* and therefore play a prominent role in the recognition of the plants in the field (Chambers 1955, p. 263). However, not infrequently, plants under field conditions are depauperate to a degree that even the diagnostic differences in achene morphology cannot be recognized (Chambers 1955, p. 264). *Under these circumstances, a taxonomic analysis based solely on herbarium specimens collected in nature will miss virtually all relevant data.*

Of course, a taxonomic analysis eventually should produce a key with which taxa can be recognized on the basis of field characters, and one may object that characters requiring us to raise the plants under controlled conditions are irrelevant for plant identification, however informative they may be. This objection misses a crucial aspect of biosystematics that I think has not been emphasized sufficiently. With the introduction of biosystematic methods, two aspects of taxonomy became increasingly separated: 1) the basic taxonomic analysis leading to the recognition and description of taxa, and 2) the practical work of identifying individual plants, i.e., assigning them to the recognized taxa.

Uropappus lindleyi flower. Copperopolis (Calaveras County, CA). Photo by Wayland Ezell.

As long as field morphology was the only source of taxonomic data, the data used for taxonomic analysis were identical with the data used for plant identification. The user of a taxonomic monograph essentially had to repeat the author's analysis under the author's guidance. With the introduction of additional data, such as the morphology under (unnaturally favorable) common garden conditions, the analytical taxonomist began looking for any and all data providing information on the (phylo)genetic relationships of the plants. Many of these characters could not be used under field conditions, so that after completing the analysis the taxonomist still faced the task of finding a set of field characters correlated with the taxa identified by other methods. The natural key to the species and subspecies of the annual *Microseris* (Chambers 1955, p. 279-280; see box on p. 34) is a heroic effort at differential diagnosis (containing negative characters such as "never white-pruinose between the ribs") in the face of a nearly random association of more or less plastic characters that change from one organ on the same plant to the next (such as achene morphology in a radial gradient across the capitulum). With the best will to provide clear and useful characters for plant diagnosis, a biosystematist has to withhold some of his analytical evidence from the user. In the end, field recognition depends on the degree to which the plants reveal their phylogenetic affiliation under field conditions.

Since the major evolutionary strategy of the annual *Microseris* seems to consist of minimizing selection among biotypes through a strong plastic adaptive response to the local conditions, the plants in nature often reveal more about the square inch of ground where they germinated than about their taxonomic affiliation. Raising them under common garden conditions clearly demonstrated

Natural Key to the Species and Subspecies

Capitula always erect; involucres imbricate, the shortest outermost phyllary at least one-fourth as long as the innermost after anthesis; paleae linear-lanceolate, bifid at the apex, silvery-scarious, deciduous; awns filiform, minutely denticulate, white; achenes dark brown or black (rarely white), the upper portion often slender-beaked.

Sect. 1 CALOCALAIS

.... 1. *M. linearifolia*

Capitula, at least in the bud, nodding or semierect; involucres imbricate or calyculate, the shortest outermost phyllary one-fourth to one-twentieth as long as the inner after anthesis; paleae various, acute to persistent; awns stouter, spiculate to barbellulate, brown or yellow; achenes black to brown, violet, tawny, or gray, the upper portion not slender-beaked.

Paleae narrowly lanceolate, more or less bifid at the apex; plants caulescent or acaulescent; involucres imbricate to nearly calyculate, one or more of the outer phyllaries lanceolate after anthesis; capitula erect or semierect when near maturity.

Sect. 2 BRACHYCARPA

Achenes blue- or red-violet to brown, tawny, or gray, never white-pruinose between the ribs, the tips of the ribs thickened and flared outward; paleae silvery-scarious or more often dull and sordid at maturity, varying from shorter to longer than the achene; embryo filling the achene or to only three-fourths as long.. 2. *M. heterocarpa*

Achenes brown to black, often minutely white-pruinose between the ribs, the tips of the ribs not thickened and flared outward; paleae silvery scarious (rarely sordid) at maturity, conspicuously shorter than the achene; embryo filling the achene.......................... 3. *M. decipiens*

Paleae various, but if narrowly lanceolate then acute at the apex; plants strictly acaulescent; involucres calyculate, all the outer phyllaries ovate or deltoid after anthesis; capitula nodding or semierect when near maturity.

Sect. 3 MICROSERIS

Pappus parts 5 or 10, paleae very thin, translucent or sordid, smooth or minutely scabrous, straight and flat at maturity, at least in the upper half, the midrib slender, linear, broadened only at the base; awns hair-like, minutely spiculate; achenes smooth or minutely scabrous on the ribs, brown to bronze or blackish, usually minutely white-pruinose between the ribs.

Pappus parts uniformly 10 ....9. *M. pygmaea*

Pappus parts uniformly 5.

Achenes 1.5-3.5 mm long, brown to blackish, never dark-spotted, columnar to obconical, the flared apex as broad as or broader than the body of the fruit; paleae 0.25-2.00 mm .... 8. *M. elegans*

Achenes 3.00-5.25 mm long (rarely to 2.5 mm), brown or bronze, often dark-spotted, columnar to clavate, the apex scarcely as broad as the body of the fruit; paleae 1-4 mm ....7. *M. bigelovii*

Pappus parts 5 or fewer; paleae thin or stout, translucent to chalky-white or sordid, minutely or distinctly scabrous to villous, arcuate, the margins incurved or convolute at maturity (flat in one species, almost obsolete in another); awns stouter, spiculate to barbellulate; achenes minutely or distinctly scabrous on the ribs, gray, tawny, brown, or blackish, rarely white-pruinose between the ribs.

Paleae linear-lanceolate, from 0.5 mm shorter to 4 mm longer than the achene, flat at maturity, the broad, very stout, and tapering midrib in each forming one-third to one-fifth of the maximum palea width; achenes never white-pruinose. .... 5. *M. acuminata*

Paleae orbicular, ovate, lanceolate, deltoid, or nearly obsolete, longer to much shorter than the achene, more or less incurved at the margins or convolute at maturity, the stout or slender midrib forming less than one-fifth of the maximum palea width in those paleae which approach the achene in length.

Paleae uniformly 5, shorter than the achene, translucent or sordid, smooth or only minutely scabrous, even to the base of the awn, the margins only slightly curled at maturity; awns spiculate; achenes gray or pale brown, sometimes white-pruinose, the ribs obtuse and lightly scabrous in the upper half, broadened and flared at the tip.......................... 6. *M. campestris*

Paleae 5 or fewer, shorter or longer than the achene, translucent to chalky or sordid, villous or scabrous, especially at the base of the awns (or usually smooth in 4b); awns spiculate or barbellulate; achenes blackish, brown, tawny, or rarely gray, never white-pruinose, the ribs scabrous, acute or obtuse in the upper half, broadened or linear at the tip.

Paleae averaging more than 1 mm long or less, sometimes nearly obsolete; ribs of the achene usually linear at the tip, not broadened nor flared outward ....4b. *M. douglasii tenella*

Paleae averaging more than 1 mm long, conspicuous; ribs of the achene usually broadened and flared outward at the tip.

Paleae scabrous, varying from 2.00 mm longer to 0.5 mm shorter than the achene; achene 4.5 mm long or less.................. .... 4c. *M. douglasii platycarpha*

Paleae scabrous to villous, varying from 1 to 6 mm shorter than the achene (or if equaling or longer than the achene, then the latter more than 4.5 mm long).. 4a. *M. douglasii douglasii*

From: Chambers, K. L. 1955. A biosystematic study of the annual species of Microseris. Contributions from the Dudley Herbarium of Stanford University 4:279-280.

the structuring of the populations in one to many more-or-less uniform biotypes, without any obvious taxonomic grouping of the biotypes (Chambers 1955, p. 266).

Breeding Behavior

Analysis of breeding behavior helped to explain this structuring of the morphological variation. In addition, the breeding behavior is relevant for analysis of species as actually or potentially interbreeding populations. Raising offspring families from single plants collected in the field clearly showed that selfing is the predominant breeding behavior in the annual species of *Microseris*: many plants produced entirely uniform offspring (Chambers 1955, p. 268), some segregated for a few characters, and very few showed a wider segregation among the offspring. Complete uniformity of offspring families meanwhile has also been confirmed with molecular markers (Roelofs and Bachmann 1995). A cladistic treatment of molecular variation among plants of a single variable population of *M. douglasii* has shown that the homozygous plants differed by essentially random recombinations of a set of common characters and formed a set of lines that were inbred for such a long time that in some of them, evolution by mutation could be demonstrated (Roelofs and Bachmann 1997). The entire population gave the impression of a set of recombinant inbred lines from across possibly dozens of generations back in time. This result not only confirmed Chambers's interpretation, it also emphasized that there was little selection among genotypes if a whole range of inbred lines was preserved in a relatively small population in which even the effects of genetic drift were likely to play a role. If recombination is very rare and selection very ineffective, we can understand the strange pattern of random distribution and association of alleles across the entire distribution range of the species in the form of homozygous lines. Because most genotypes seem to have a high chance of persisting anywhere within the range of the species, combination of three factors are sufficient to distribute alleles randomly throughout the species: 1) virtually no local gene exchange, 2) effectively unlimited gene exchange throughout the range of the species, by means of extremely rare dispersal events, sometimes over hundreds of miles (Van Heusden and Bachmann 1992a, 1992b), and 3) extremely rare outcrossing.

The crucial interpretation is that the plants involved in this extremely slow but very effective allele exchange are the "significant evolutionary units" that can be recognized as species. How many are there?

With morphology as a sole guide, the only approach to this problem would have been a thorough listing, character by character and biotype by biotype, of the distribution of the polymorphic characters in order to detect matching borders for intraspecific polymorphisms (as the next best criteria in the virtual absence of species-specific diagnostic characters). At some time, appropriate molecular characters may make this approach possible, but Chambers did not even consider it, knowing it would have foundered due to the many trans-specific polymorphisms, especially in plants of hybrid origin. He selected the two non-morphological methods capable of detecting species limits within the mass of biotypes: chromosome counts and studies of hybrid fertility.

Allopolyploids and Their Diploid Parents

Polyploidy and the origin of hybrid allopolyploid species were well understood (Winge 1917), and chromosome counting was a routine part of biosystematic investigations. Chromosome counts of a few species of *Microseris* had just been published (Stebbins *et al.* 1953), and the existence of tetraploid species (2n=36) had been documented. Intensive chromosome counts of a sufficient sample of accessions allowed Chambers to determine the ploidy of all species, and, in fact, was a major help in recognizing species, especially in mixed populations. The discovery of a tetraploid taxon, *M. campestris,* frequently co-occurring and sharing characters with both *M. douglasii* and *M. elegans,* significantly helped to differentiate among the three taxa (Chambers 1955, p. 243, 249). Another taxon, *M. acuminata,* identified as a tetraploid by Stebbins *et al.* (1953), was recognizable by its relatively uniform morphology, but its parentage was not clear. Two alloploid taxa, *M. heterocarpa* and *M. decipiens,* were obvious derivatives of *M. lindleyi* (then called *M. linearifolia*) with *M. douglasii* and *M. bigelovii*, respectively, contributing the second genome. Since *M. lindleyi* morphologically is so strikingly different from the other annual species, the fact that it participates in the polyploid complex of the annual species of *Microseris* was the decisive factor in retaining it in the genus (Chambers 1955, p. 217). It took another 36 years before the first DNA data on the (chloroplast) phylogeny of *Microseris* showed that *M. lindleyi* does not form a monophyletic group with the other annual species of the genus (Wallace and Jansen 1990), but is at the basis of a clade also containing the genera *Nothocalais* and *Agoseris* (Jansen *et al.* 1991). On the basis of this result, Nuttall's 1841 name *Uropappus lindleyi,* was resurrected for *M. lindleyi.* As a consequence, *M. heterocarpa* and *M. decipiens* became intergeneric hybrids and were separated by Chambers as a new genus, *Stebbinsoseris* (Jansen *et al*. 1991), in honor of G. Ledyard Stebbins, who, together with James Jenkins and Marta Walters, had first recognized the allopolyploid nature of *S. heterocarpa* (Stebbins *et al.* 1953).

In 1955 Chambers was fully aware of the doubtful status of *U. lindleyi* (then called *M. linearifolia*, see Chambers 1964) and the fact that it (repeatedly) formed allopolyploids with annual

Urpopappus lindleyi fuiting head showing bristle-tipped pappus scales. Copperopolis, CA. Photo by Wayland Ezell.

Microseris (p. 217). Even with hindsight, we have to conclude that the proper cladistic position of *U. lindleyi* could not be determined with morphological characters. The close relationship with *Agoseris* was a distinct possibility (Chambers, pers. comm., 1976). With the combined data available in 1955 permitting no definite conclusion, Chambers's decision to retain all three species in *Microseris* was based on parsimony: no intergeneric hybrids had to be postulated and named as long as there was no compelling evidence for them.

It took even longer before new evidence on the parentage of *M. acuminata* became available by sequence analysis of the internal transcribed spacer (ITS) of the nuclear genes for ribosomal RNA (rDNA) (Roelofs *et al.* 1997). The discussion of the problem by Chambers deserves to be quoted (Chambers 1955, p. 234):

> *On morphological grounds,* Microseris acuminata *cannot be considered an autopolyploid derived from any existing species, and a hybrid origin is definitely indicated. However, it does not appear to be a hybrid between any two diploid biotypes occurring at the present time...*

In fact, the single ITS sequence found in *M. acuminata* has to be interpreted as a recombinant sequence between that of *M. douglasii* and an extinct second taxon. Surprisingly, this extinct second taxon, together with *M. elegans*, also is a parent of *M. campestris*. This interpretation is based on six "synapomorphic" nucleotide mutations between two clearly independent allotetraploid species. Aside from that, the postulated taxon is very elusive. Both tetraploid species are monomorphic for a widely distributed chloroplast genome typical for *M. douglasii* (Roelofs *et al*. 1997), and even though the ITS sequence of the extinct ancestor does not contain a single one of the six autapomorphic nucleotides of *M. douglasii*, the nuclear genome of the extinct species must have contained all the characters common to *M. campestris* and *M. douglasii*, and absent in *M. elegans*. Before the molecular results, no evidence led to suspicions of an unknown ancestor of *M. campestris*, nor of a shared parent with *M. acuminata*. Thus the molecular evidence that resolved known problems with *U. lindleyi* and *M. acuminata* also revealed that the true situation with *M. campestris* is much more complex than indicated by morphological characters.

Hybrid Fertility and Natural Hybridization

The identification of polyploids helped sort out diploid taxa and revealed one of the sources of hybrid sterility in crosses between individuals from various taxa. Crossing experiment diagrams are a typical feature of biosystematic monographs even today (Brunell and Whitkus 1999). Chambers' analysis shows near-sterility in crosses with *U. lindleyi,* and reduced, but highly variable fertility in crosses among *M. douglasii*, *M. bigelovii* and *M. elegans* (Chambers 1955, p. 262). Later, crosses with *M. pygmaea* also produced F1 hybrids with variable fertility (Chambers 1963, and unpublished). Meiotic analysis of F1 hybrids has shown that the reduced fertility of the hybrids is due to reduced chromosome homology, and this was confirmed later by segregation analysis in selfed offspring of interspecific hybrids (Bachmann and Hombergen 1996, 1997).

All crossing experiments have confirmed the close genetic relationship of the biotypes assigned by Chambers to a species and the marked but never absolute sterility barriers among species at the diploid level. Since the fact that the plants reproduce nearly exclusively by selfing does not seem to have restricted intraspecific variation, and since there are allopolyploid hybrids in various combinations, it also is very likely that diploid interspecific hybrids will be formed. Against the background of the confusing intraspecific morphological variation, it is practically impossible to identify diploid species hybrids or hybrid offspring by an intermediate morphology. Still, with his very detailed knowledge of the variability within and among species, Chambers has suggested that at the two localities where the geographic ranges of *M. douglasii* and *M. bigelovii* overlap (at the coast in and near San Francisco and between San Luis Obispo and Morro Bay in San Luis Obispo County), plants with an intermediate morphology are found (Chambers 1955, p. 232).

The suggestion of introgression between these two species has been confirmed in a very surprising way following the phylogenetic analysis of chloroplast DNA. The four restriction site mutants found by Wallace and Jansen (1990) in chloroplasts of the annual taxa (excluding *U. lindleyi*) did not fit the proposed relationship of the species. Given the general conservative and phylogenetically informative nature of cpDNA variation at this level, the result was examined in detail (Roelofs and Bachmann 1997). Eventually, we found 13 markers that supported the discrepancy between nuclear (organismic) and chloroplast phylogenies and strongly suggested several routes of interspecific transfer of chloroplasts among the diploid annuals. One of these concerns the introgression of chloroplasts from *M. bigelovii* into *M. douglasii*, and it involves both the San Francisco and the San Luis Obispo populations of

Microseris howellii flower. Rough and Ready Botanical Wayside. Endemic to Illinois River Valley in Curry and Josephine counties, Oregon. Photo by Charlene Simpson.

M. douglasii, a region where the genetic material of *M. bigelovii* seems to have penetrated deeply into the range of *M. douglasii*. Similarly, there is introgression of *M. douglasii* chloroplasts into *M. elegans* (Roelofs and Bachmann 1997). Even more striking, a chloroplast genome ancestral to those of *M. bigelovii* and *M. pygmaea* seems to have introgressed into *M. douglasii* from the common ancestor of the two species. A fourth chloroplast genome in *M. douglasii* coincides with the subspecies *M. d. platycarpha* recognized by Chambers (1955) and supports his interpretation of three discernible, but not clearly delimitated, morphological units within *M. douglasii* as lines that are intergrading after initial differentiation (Chambers 1955, p. 229-230).

Conclusion

I was able to use Chambers's monograph to evaluate of the achievements and limitations of classical biosystematics for two reasons. One is the large volume of subsequent research into species differentiation based on this monograph; the other is the remarkable quality of the work that allows us to recognize its limitations and weaknesses as those of the discipline at the time, not those of the author. Chambers was very explicit about the limitations of his methods. Much of the work in my laboratory for the last 25 years has dealt with *Microseris,* and I consider it significant that, until molecular methods, none of our findings have contradicted Chambers's conclusions. Time and again we have added details confirming and extending his work. A remarkable example is his suggestion that the tetraploid *M. scapigera* of Australia and New Zealand is an allotetraploid hybrid between a North American perennial (large chromosomes) and an annual species (small chromosomes) (Chambers 1955, p. 248-249). That a very successful Southern Hemisphere species should be a hybrid between two North American taxa with different ecological and geographical distributions was borne out when the chloroplast genome of *M. scapigera* appeared to be an early offshoot of the "annual" chloroplast clade (Wallace and Jansen 1990) and when the single nuclear ITS sequence of *M. scapigera* was shown to recombine features from the perennial and the annual species (Van Houten *et al*. 1993).

I hope to have shown that biosystematics was essential for the success of Chambers' analysis. Morphology still played a prominent role in his work, but the interpretation of the morphological patterns was guided by crucial additional information and not completely a result of an instinctively correct assessment of the weight of various morphological characters. Taxonomic units that Chambers proposed as species in *Microseris* have a clearly defined biological meaning and are likely to survive any further examination. A few of Chambers's conclusions have been modified by molecular evidence of a kind that taxonomists in 1955 could hardly have imagined, but more of his results were confirmed.

References

Bachmann, K. 1998. Species as units of diversity: an outdated concept. Theory in the Biosciences 117:213-230.

Bachmann, K. and J. Battjes. 1994. Variability in a predominantly self-fertilizing annual with fragmented distribution, *Microseris douglasii* (Asteraceae: Lactuceae). Biologisches Zentralblatt 113:69-95.

Bachmann, K., K.L. Chambers, and H.J. Price. 1979. Genome size and phenotypic evolution in *Microseris* (*Asteraceae, Cichorieae*). Plant Systematics and Evolution Supplement 2:41-66.

Bachmann, K, K.L. Chambers, and H.J. Price. 1984. Differential geographic distribution of spatulate and pointed leaf shapes in *Microseris bigelovii* (Asteraceae-Lactuceae). Beiträge zur Biologie der Pflanzen 59:5-14.

Bachmann, K. and E.-J. Hombergen. 1996. Mapping genes for phenotypic variation in *Microseris* (Lactuceae) with molecular markers. Pages 23-43 in P.D.S. Caligari and D.J.N. Hind, editors. *Compositae: Biology and Utilization*. Royal Botanic Garden, Kew, England.

Bachmann, K. and E.-J. Hombergen. 1997. From phenotype via QTL to virtual phenotype in *Microseris* (Asteraceae): predictions from multilocus marker genotypes. New Phytologist 137:9-18.

Bachmann, K. and H.J. Price. 1977. Repetitive DNA in Cichorieae. Chromosoma 61:267-275.

Battjes, J. 1994. Determination of organ numbers during inflorescence development of *Microseris* (Asteraceae: Lactuceae). PhD thesis, University of Amsterdam, The Netherlands.

Battjes, J. and K. Bachmann. 1994. Phenotypic plasticity of capitulum morphogenesis in *Microseris pygmaea* (Asteraceae: Lactuceae). Annals of Botany 73:299-305.

Brunell, M.S. and R. Whitkus. 1999. Analysis of cross-compatibility in *Eriastrum densifolium* (Polemoniaceae). Plant Systematics and Evolution 215:241-254.

Chambers, K.L. 1955. A biosystematic study of the annual species of *Microseris.* Contributions from the Dudley Herbarium of Stanford University 4:207-312.

Chambers, K.L. 1963. Amphitropical species pairs in *Microseris* and *Agoseris* (Compositae: Cichorieae). Quarterly Review of Biology 38:124-140.

Chambers, K.L. 1964. The nomenclature of *Microseris Lindleyi* (DC.) Gray. Leaflets of Western Botany 10:106-108.

Chambers, K.L. 1995. The contributions of Göte Turesson to plant taxonomy. Pages 37-55 in A.R. Kruckeberg, R.B. Walker, and A.E. Leviton, editors. Genecology and ecogeographic races. Pacific Division of AAAS, San Francisco, CA.

Clausen, J., D.D. Keck, and W.M. Hiesey. 1948. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Institute of Washington Publication 520.

Don, D. 1832. Descriptive catalogue of the compositae contained in the herbarium of Dr. Gillies; with some additions from other sources. Philosophical Magazine, new series 11:387-388.

Feuer, S. and A.S. Tomb. 1977. Pollen morphology and the detailed structure of family Compositae, tribe Cichorieae. II. Subtribe Microseridinae. American Journal of Botany 64:230245.

Gailing, 0., E.J. Hombergen, and K. Bachmann. 1999. QTL mapping reveals specific genes for the evolutionary reduction of microsporangia in *Microseris* (Asteraceae). Plant Biology 1:219-225.

Gould, S.J. 1982. Introduction. Pages xvii-xli in Th. Dobzhansky. Genetics and the origin of species, new edition of the first edition. Columbia University Press, New York.

Greene, E.L. 1905. A new study of *Microseris.* Pittonia 5:4-16.

Hagen, J. B. 1983. The development of experimental methods in plant taxonomy, 1920-1950. Taxon 32:406-416.

Hall, H.M. and F.E. Clements. 1923. The phylogenetic method in taxonomy. The North American species of *Artemisia, Chrysothamnus,* and *Atriplex*. Carnegie Institute of Washington Publication 326.

Harborne, J.B. 1977. Variations in pigment patterns in *Pyrrhopappus* and related taxa of the Cichorieae. Phytochemistry 16:927-928.

Hobbs, R.J. 1985. Harvester ant foraging and plant species distribution in annual grassland. Oecologia 67:519-523.

Hooker, J.D. 1853. The botany of the Antarctic voyage of H.M. Discovery ships Erebus and Terror in the years 1839-1843. II. Flora Novae-Zelandiae, part 1, flowering plants. No. 2:81-160. Lovell Reeve, London, England.

Hull, D.L. 1997. The ideal species concept - and why we can't get it. Pages 357-380 in M.F. Claridge, A.H. Dawah, and M.R. Wilson, editors. *Species. The Units of Diversity.* Chapman and Hall, London, England.

Irmler, C., K. Bachmann, K.L. Chambers, H.J. Price, and A. König. 1982. Enzymes and quantitative morphological characters compared between the allotetraploid *Microseris decipiens* and its diploid parental species. Beiträge zur Biologie der Pflanzen 57:269-289.

Jansen, R.K., R.S. Wallace, K.-J. Kim, and K.L. Chambers. 1991. Systematic implications of chloroplast DNA variation in the subtribe Microseridinae (Asteraceae: Lactuceae). American Journal of Botany 78:1015-1027.

Jepson, W.L. 1957. A Manual of the Flowering Plants of California. University of California Press, Berkeley and Los Angeles.

Mauthe, S. 1984. Genetische Komponenten bei der Köpfchenentwicklung von *Microseris douglasii* (Asteraceae-Lactuceae). PhD thesis, University of Heidelberg, Germany.

Nagl, W. and K. Bachmann. 1980. Condensed chromatin in diploid and allopolyploid *Microseris* species with different genome sizes: a quantitative electron microscopic study. Theoretical and Applied Genetics 57:107-111.

Oud, J.L., F. Schuring, and C. Berg. 1988. The karyotype of *Microseris bigelovii*, *M. douglasii*, and *M. pygmaea* (Asteraceae). Plant Systematics and Evolution 159:249-256.

Pickett, F.B. and D.R. Meeks-Wagner. 1995. Seeing double: appreciating genetic redundancy. The Plant Cell 7:1347-1356.

Price, H.J. and K. Bachmann. 1975. DNA content and evolution in the Microseridinae. American Journal of Botany 62:262-267.

Price, H.J. and K. Bachmann. 1976. Mitotic cycle time and DNA content in annual and perennial *Microseridinae* (*Compositae*, *Cichorieae*). Plant Systematics and Evolution 126:323-330.

Price, H.J. , K.L. Chambers, and K. Bachmann. 1981. Geographic and ecological distribution of genomic DNA content variation in *Microseris douglasii* (Asteraceae). Botanical Gazette 142:415-426.

Roelofs, T.F.M. 1996. Is *Microseris douglasii* paraphyletic? Nuclear phylogeny versus chloroplast phylogeny. PhD thesis, University of Amsterdam, The Netherlands.

Roelofs, D. and K. Bachmann. 1995. Chloroplast and nuclear DNA variation among homozygous plants in a population of the autogamous annual *Microseris douglasii (Asteraceae, Lactuceae).* Plant Systematics and Evolution 196:185-194.

Roelofs, D. and K. Bachmann. 1997. Comparison of chloroplast and nuclear phylogeny in the autogamous annual *Microseris douglasii* (*Asteraceae: Lactuceae*). Plant Systematics and Evolution 204:49-63.

Roelofs, D., J. Van Welzen, P. Kuperus, and K. Bachmann. 1997. Molecular evidence for an extinct parent of the tetraploid species *Microseris acuminata* and *M. campestris* (Asteraceae, Lactuceae). Molecular Ecology 6:641-649.

Rollins, R. 1952. Taxonomy today and tomorrow. Rhodora 54:1-19.

Schultz-Bipontinus, C.H. 1866. Beitrag zum System der Cichorieen. Pollichia 22-24:305-310.

Sneddon, B.V. 1977. A biosystematic study of *Microseris* subgenus *Monermos* (Compositae: Cichorieae). Dissertation, University of Wellington, New Zealand.

Stebbins. G.L., Jr., J.A. Jenkins, and M.S. Walters. 1953. Chromosomes and phylogeny in the Compositae tribe Cichorieae. University of California Publications in Botany 26:401-430.

Turesson, G. 1923. The scope and import of genecology. Hereditas 4:171-176.

Van Heusden, A.W. 1990. Genetic analysis of natural variation in *Microseris pygmaea* (Asteraceae) in crosses with *M. bigelovii* C93b. PhD thesis, University of Amsterdam, The Netherlands.

Van Heusden, A.W. and K. Bachmann. 1992a. Genotype relationships in *Microseris elegans* (*Asteraceae, Lactuceae*) revealed by DNA amplification from arbitrary primers (RAPDs). Plant Systematics and Evolution 179:221-233.

Van Heusden, A.W. and K. Bachmann. 1992b. Nuclear DNA polymorphisms among strains of *Microseris bigelovii* (Asteraceae: Lactuceae) amplified from arbitrary primers. Botanica Acta 105:331-336.

Van Houten, W. 1994. Nuclear DNA characters for the analysis of evolution in *Microseris.* PhD thesis, University of Amsterdam, The Netherlands.

Van Houten, W.H.J., N. Scarlett, and K. Bachmann. 1993. Nuclear DNA markers of the Australian tetraploid *Microseris scapigera* and its North American relatives. Theoretical and Applied Genetics 87:498-505.

Van Houten, W.H.J., A.W. Van Heusden, J. Rouppe van der Voort, L. Raijmann, and K. Bachmann. 1991. Hypervariable DNA fingerprint loci in *Microseris pygmaea* (Asteraceae, Lactuceae). Botanica Acta 104: 252-256.

Vlot, E.C. 1993. Genetic and plastic variation in meristic characters of the capitulum of *Microseris douglasii* (Asteraceae). PhD thesis, University of Amsterdam, The Netherlands.

Wagenitz, G. 1996. Von der Gestalt zum Molekül - der Weg der Systematik? Pages 88-97 in R. Fritsch and K. Hammer, editors. *Evolution und Taxonomie von pflanzengenetischen Ressourcen. Zentralstelle für Agrardokumentation und -information*, Bonn, Germany.

Wallace, R.S. and R.K. Jansen. 1990. Systematic implications of chloroplast DNA variation in the genus *Microseris* (Asteraceae: Lactuceae). Systematic Botany 15:606-616.

Winge, Ø. 1917. The chromosomes, their numbers and general importance. Comptes Rendus des Travaux du Laboratoire Carlsberg (Serie Physiologie) 23:41-74.

Zentgraf, J. 1986. Genetische Aspekte der Köpfchenentwicklung bei Hybriden der annuellen Arten *Microseris pygmaea* und *Microseris bigelovii* (Asteraceae-Lactuceae). PhD thesis, University of Heidelberg, Germany.

Dr. Konrad Bachmann is head of the Department of Taxonomy at the Institut für Pflanzengenetik und Kulturpflanzenforschung in Gatersleben, Germany. He started his work on the genetics of *Microseris* as an Associate Professor at the University of South Florida, Tampa, and continued it in his subsequent positions at the University of Heidelberg, Germany, where Ken Chambers visited him in 1983, and the University of Amsterdam, The Netherlands, before moving to his present position.

Appendix 1. Graduate students and their thesis titles directed by Kenton L. Chambers at Oregon State University, listed in chronological order.

Curt G. Carlbom, MS, 1964. An Experimental Taxonomic Study of a Northwest American Polyploid Species, *Scrophularia lanceolata*.

Leslie D. Gottlieb, MS, 1965.Hybridization Between *Arctostaphylos viscida* and *A. canescens* in Oregon.

Curt G. Carlbom, PhD, 1966. A Biosystematic Study of Some North American Species of *Agrostis* and *Podagrostis*.

Milton L. Dean, PhD, 1966. A Biosystematic Study in the Genus *Aster* Section *Aster* in Western North America.

Ronald J. Tyrl, MS, 1967. Cytogeography of *Achillea millefolium* L. in Western Oregon.

James R. Estes, PhD, 1967. Cytotaxonomic Studies in the *Artemisia ludoviciana* Polyploid Complex of the Pacific Northwest.

Ronald J. Tyrl, PhD, 1969. Origin and Distribution of Polyploid *Achillea* in Western North America.

Wayland L. Ezell, PhD, 1970. Biosystematics of the *Mimulus nanus* Complex in Oregon.

Allan H. Legge, PhD, 1971. The Gene-ecology of *Crepis nana* and *Crepis elegans* in Arctic and Alpine North America.

Dennis R. Jaques, MS, 1973. Reconnaissance Botany of Alpine Ecosystems of Prince of Wales Island, Southeast Alaska.

Robert L. Carr, PhD, 1973. A Taxonomic Study in the Genus *Hackelia* in Western North America.

Judith Glad, MS, 1975. Taxonomy and Ecology of *Mentzelia mollis* Peck and Related Species.

John M. Miller, MS, 1975. Polymorphic, Sympatric Flavonoid Variants of *Claytonia perfoliata* Donn.

Harold L. Lint, PhD, 1977. Revision of *Juncus* Subgenus *Genuini* (Juncaceae) in the Pacific States.

Hesh J. Kaplan, PhD, 1977. A Chemosystematic Study of the Phylogenetic Position of *Arabidopsis thaliana* (Brassicaceae) Employing Numerical Methods.

Dennis D. Thompson, MS, 1977. Taxonomic Studies of the *Eucephalus* Complex of *Aster* in the Pacific Northwest.

Cheryl Crowder, MS, 1978. The Ecology and Reproduction of *Sophora leachiana* Peck (Fabaceae).

John M. Miller, PhD, 1978. Phenotypic Variation in Diploid and Tetraploid Populations of *Claytonia perfoliata* (Portulacaceae).

Richard Halse, PhD, 1979. Taxonomy of *Phacelia* Section *Miltitzia* (Hydrophyllaceae).

Geraldine A. Guppy, PhD, 1980. Biosystematics of a Western North American Polyploid Complex in the Genus *Aster*.

Maria J.P. Pires, MS, 1980. Morphogenetic Studies of Intraspecific Hybrids of *Microseris laciniata* (Hook.) Sch.-Bip.

Steven Broich, PhD, 1983. A Systematic Study of *Lathyrus vestitus* Nutt. ex T. & G. (Fabaceae) and Allied Species of the Pacific Coast.

Elaine Joyal, MS, 1983. Ecology and Reproduction in *Collomia macrocalyx* Brand (Polemoniaceae).

J. Stephen Shelly, MS, 1985. Biosystematic Studies of *Phacelia capitata* (Hydrophyllaceae), a Species Endemic to Serpentine Soils in Southwestern Oregon.

Nancy Fredricks, MS, 1986. *Calochortus howellii*: Ecology of a Rare Serpentine Endemic and Comparison with the New Species, *C. umpquaensis* (Liliaceae).

Edward R. Alverson, MS, 1989. Biosystematics of Parsley-Ferns, *Cryptogramma* R. Br., in Western North America.

Thomas N. Kaye, MS, 1989. Autecology, Reproductive Ecology, and Demography of *Astragalus australis* var. *olympicus* (Fabaceae).

Carolyn Wright, MS, 1990. A Systematic and Ecological Study of *Astragalus diaphanus* (Fabaceae).

Robert J. Meinke, PhD, 1992. Systematic and Reproductive Studies of *Mimulus* (Scrophulariaceae) in the Pacific Northwest: Implications for Conservation Biology.

Nancy Fredricks, PhD, 1992. Population Biology of Rare Mariposa Lilies (*Calochortus*: Liliaceae) Endemic to Serpentine Soils in Southwestern Oregon.

Karen E. (Solonika) Bledsoe, MS, 1993. Morphological and Cytological Variation in *Trillium albidum* Freeman (Liliaceae).

Laura A. Morrison, PhD, 1994. Reevaluation of Systematic Relationships in *Triticum* L. and *Aegilops* L. Based on Comparative Morphological and Anatomical Investiga-

Appendix 2. Publications by Kenton L. Chambers. Titles including technical papers and abstracts, taxonomic treatments, book reviews, and articles for amateur botanists (listed in chronological order).

Chambers, K.L. 1955. A biosystematic study of the annual species of *Microseris*. Contributions from the Dudley Herbarium of Stanford University 4:207-312.

Chambers, K.L. 1955. A collection of plants from the eastern flank of the Sierra San Pedro Martir, Baja California. Contributions from the Dudley Herbarium of Stanford University 4:323-330.

Chambers, K.L. 1957. Taxonomic notes on some Compositae of the western United States. Contributions from the Dudley Herbarium of Stanford University 5:57-68.

Chambers, K.L. 1957. Plant classification (a review). Scientific Monthly 85:331.

Stern, W.L., G.K. Brizicky, and K.L. Chambers. 1958. A collection of woody plants from Panama. Tropical Woods 109:61-80.

Chambers, K.L. 1960. *Nothocalais* and *Microseris*. Pages 552-562 in L. Abrams and R.S. Ferris, editors. *Illustrated Flora of the Pacific States*, vol. IV. Stanford University Press, Stanford, CA.

Chambers, K.L. 1960. Evolution in a family of angiosperms (a review). Ecology 41:601-602.

Chambers, K.L. 1960. On the origin of an unusual *Dipholis* from the Florida Keys. Tropical Woods 112:40-57.

Stern, W.L. and K.L. Chambers. 1960. The citation of wood specimens and herbarium vouchers in anatomical research. Taxon 9:7-13.

Chambers, K.L. 1961. Plant cytotaxonomy. Pp. 789-790 in Peter Gray, ed. *Encyclopedia of the Biological Sciences*. Reinhold Book Division.

Chambers, K.L. 1961. Evolutionary trends in the Cichorieae (abstract). American Journal of Botany 48:545.

Chambers, K.L. 1962. Wild flowers of Oregon (pamphlet). Oregon State Highway Department.

Chambers, K.L. 1962. Amphitropical relationships in the herbaceous flora of the Pacific coast: Species pairs in the Cichorieae (abstract). American Journal of Botany 49:674-675.

Chambers, K.L. 1963. Plant marvels in miniature (a review). Plant Science Bulletin 9:6-7.

Chambers, K.L. 1963. *Claytonia nevadensis* in Oregon. Leaflets of Western Botany 10:1-8.

Chambers, K.L. 1963. *Hedyotis australis* in Georgia. Rhodora 65:271-273.

Chambers, K.L. 1963. Amphitropical species pairs in *Microseris* and *Agoseris* (Compositae, Cichorieae). Quarterly Review of Biology 38:124-140.

Chambers, K.L. and L.J. Dennis. 1963. New distributions for four grasses in Oregon. Madroño 17:91-92.

Chambers, K.L. 1964. *Saxifraga eschscholtzii* Sternb. Madroño 17:203-204.

Chambers, K.L. 1964. Nomenclature of *Microseris lindleyi*. Leaflets of Western Botany 10:106-108.

Chambers, K.L. 1964. Genetic relationships among three allopatric species of *Microseris* (abstract). American Journal of Botany 51:687.

Chambers, K.L. 1965. An allopolyploid *Krigia* from the southern Appalachians (abstract). American Journal of Botany 52:648.

Chambers, K.L. 1965. Flower pollination in the Phlox family (a review). Science 150:872-873.

Chambers, K.L. 1966. Vascular plants of the Pacific Northwest, part 2 (a review). Quarterly Review of Biology 41:212-213.

Chambers, K.L. 1966. Evolution and systematics (a review). BioScience 16:556-557, 560.

Chambers, K.L. 1966. Notes on some grasses of the Pacific Coast. Madroño 18:250-251.

Chambers, K.L. 1969. The systematics of populations in plants - discussant's remarks. Proceedings of the Conference on Systematic Biology, National Academy of Sciences. National Research Council, Washington, DC.

Chambers, K.L. 1969. Flora of Alaska and neighboring territories (a review). Madroño 20:78-80.

Chambers, K.L. 1969. Hummingbirds and their flowers (a review). Plant Science Bulletin 15:11.

Chambers, K.L. 1969. Flora of the Queen Charlotte Islands, parts I and II (a review). The Bryologist 72:428-429.

Chambers, K.L., editor. 1970. Biochemical Coevolution. Proceedings of the Biology Colloquium. Oregon State University Press, Corvallis.

Chambers, K.L. 1971. Pages 39-40 in The systematic biology collections of the United States: An essential resource, part I (a review). Museum News, June 1971.

Chambers, H.L. and K.L. Chambers. 1971. Artificial and natural hybrids in *Pycnanthemum*. Brittonia 23:71-88.

Chambers, K.L. 1972. (Introduction to) E.L. Horn. *Wildflowers 1: The Cascades.* The Touchstone Press, Beaverton, OR.

Chambers, K.L. 1973. The floristic relationship of Onion Peak with Saddle Mountain, Clatsop County, Oregon. Madroño 22:105-114.

Chambers, K.L. and L.J. Dennis. 1973. Additional plant records for Oregon. Madroño 22:149-150.

Chambers, K.L. 1974. Notes on the flora of Clatsop County, Oregon. Madroño 22:278-279.

Chambers, K.L. 1975. A flora of the Trinity Alps of northern California (a review). Torreya 102:31-32.

Fellows, C.E. and K.L. Chambers. 1976. Nomenclatural notes on *Claytonia spathulata*. Madroño 23:297-299.

Chambers, K.L. 1977. Threatened and endangered species problems in North America: The northwestern United States. Pages 45-49 in G.T. Prance and T.S. Elias, editors. *Extinction is Forever.* New York Botanical Garden, New York.

Chambers, K.L. 1977. Morton E. Peck Herbarium. Taxon 26:160-161.

Miller, J.M. and K.L. Chambers. 1977. Chromosome numbers and relationships of *Claytonia saxosa* and *C. arenicola* (Portulacaceae). Madroño 24:62-63.

Bachmann, K. and K.L. Chambers. 1978. Pappus-part number in annual species of *Microseris* (Compositae, Cichorieae). Plant Systematics and Evolution 129:119-134.

Tomb, A.S., K.L. Chambers, D.W. Kyhos, A.M. Powell, and P.H. Raven. 1978. Chromosome numbers in the Compositae. XIV. Lactuceae. American Journal of Botany 65:717-721.

Bachmann, K., K.L. Chambers, and H.J. Price. 1979. Genome size and phenotypic evolution in *Microseris* (Asteraceae, Cichorieae). Plant Systematics and Evolution Supplement 2:41-66.

Siddall, J.L., K.L. Chambers, and D.H. Wagner. 1979. Rare, threatened and endangered vascular plants in Oregon - An interim report. Oregon Natural Area Preserves Advisory Committee, Oregon State Land Board.

Price, H.J., K. Bachmann, K.L. Chambers, and J. Riggs. 1980. Detection of intraspecific variation in DNA content in *Microseris douglasii*. Botanical Gazette 141:195-198.

Bachmann, K. and K.L. Chambers. 1981. Genes regulating the appearance of two kinds of fruits in *Microseris* strain B87 (Asteraceae). Experientia 37:29-31.

Bachmann, K., K.L. Chambers, and H.J. Price. 1981. Genetic determination of pappus-part number in the annual hybrid *Microseris* B87 (Asteraceae-Lactuceae). Plant Systematics and Evolution 138:235-246.

Price, H.J., K.L. Chambers, and K. Bachmann. 1981. Genome size variation in diploid *Microseris bigelovii* (Asteraceae). Botanical Gazette 142:156-159.

Price, H.J., K.L. Chambers, and K. Bachmann. 1981. Geographic and ecological distribution of genomic DNA content variation in *Microseris douglasii* (Asteraceae). Botanical Gazette 142:415-426.

Bachmann, K., K.L. Chambers, H.J. Price, and A. König. 1982. Four additive genes determining pappus-part numbers in *Microseris* annual hybrid C34 (Asteraceae, Lactuceae). Plant Systematics and Evolution 141:123-141.

Mauthe, S., K. Bachmann, K.L. Chambers, and H.J. Price. 1982. Variation of the inflorescence among populations of *Microseris laciniata* (Asteraceae). Beiträge zur Biologie der Pflanzen 56: 25-52.

Allen, G.A., M.L. Dean, and K.L. Chambers. 1983. Hybridization studies in the *Aster occidentalis* (Asteraceae) polyploid complex of western North America. Brittonia 35:353-361.

Bachmann, K., K.L. Chambers, H.J. Price, and A. König. 1983. Spatulate leaves: a marker gene for the evolution of *Microseris bigelovii* (Asteraceae). Beiträge zur Biologie der Pflanzen 57:167-179.

Dean, M.L. and K.L. Chambers. 1983. Chromosome numbers and evolutionary patterns in the *Aster occidentalis* polyploid complex (Asteraceae) of western North America. Brittonia 35:189-196.

Irmler, C., K. Bachmann, K.L. Chambers, H.J. Price, and A. König. 1983. Enzymes and quantitative morphological characters compared between the allotetraploid *Microseris decipiens* and its diploid parental species. Beiträge zur Biologie der Pflanzen 57:269-289.

Price, H.J., K.L. Chambers, K. Bachmann, and J. Riggs. 1983. Inheritance of nuclear 2C DNA content variation in intraspecific and interspecific hybrids of *Microseris* (Asteraceae). American Journal of Botany 70:1133-1138.

Bachmann, K., K.L. Chambers, and H.J. Price. 1984. A second marker enzyme in the genetics of pappus-part numbers in *Microseris* hybrid B87 (Asteraceae, Lactuceae). Plant Systematics and Evolution 145:243-258.

Bachmann, K., K.L. Chambers, and H.J. Price. 1984. Genetic components of heterocarpy in *Microseris* hybrid B87 (Asteraceae, Lactuceae). Plant Systematics and Evolution 148:149-164.

Bachmann, K., K.L. Chambers, and H.J. Price. 1984. Differential geographic distribution of spatulate and pointed leaf shapes in *Microseris bigelovii* (Asteraceae, Lactuceae). Beiträge zur Biologie der Pflanzen 59:5-14.

Chambers, K.L. 1984. *Oenothera wolfii* in Oregon. Bulletin of the Native Plant Society of Oregon 17(10):9-11.

Miller, J.M., K.L. Chambers, and C.E. Fellows. 1984. Cytogeographic patterns and relationships of the *Claytonia sibirica* complex (Portulacaceae). Systematic Botany 9:266-271.

Price, H.J., K.L. Chambers, and K. Bachmann. 1984. Environmental stress and nuclear DNA content of *Microseris douglasii.* Genetics 107:85.

Zentgraf, J., K. Bachmann, and K.L. Chambers. 1984. Single-gene heterozygotes derived from the polygenic pappus-part system of *Microseris* hybrid C34 (Asteraceae, Lactuceae). Plant Systematics and Evolution 147:205-226.

Bachmann, K., K.L. Chambers, J. Grau, and H.J. Price. 1985. Genetic variation in *Microseris pygmaea* (Asteraceae - Lactuceae). Beiträge zur Biologie der Pflanzen 60:51-58.

Bachmann, K., K.L. Chambers, and H.J. Price. 1985. Genome size and natural selection: observations and experiments in plants. Pages 263-272 in T. Cavalier-Smith, editor. *DNA and Evolution: Natural Selection and Genome Size*. John Wiley & Sons, New York.

Bachmann, K., A.W. van Heusden, K.L. Chambers, and H.J. Price. 1985. Duplications of additively acting genes in the evolution of a plant (*Microseris pygmaea*). Experientia 41:1348-1350.

Chambers, K.L. 1985. Plants can change their names. Bulletin of the Native Plant Society of Oregon 18(1):6-7.

Chambers, K.L. 1985. When is a variety a subspecies? Bulletin of the Native Plant Society of Oregon 18(4):43 & 46.

Chambers, K.L. 1985. How should wheatgrasses be classified? Bulletin of the Native Plant Society of Oregon 18(5):54-55.

Chambers, K.L. 1985. Pitfalls in identifying *Ventenata dubia*. Madroño 32:120-121.

Hammond, P.C. and K.L. Chambers. 1985. A new species of *Erythronium* (Liliaceae) from the Coast Range of Oregon. Madroño 32:49-56.

Mauthe, S., K. Bachmann, K.L. Chambers, and H.J. Price.

1985. Inheritance of heterocarpy in *Microseris douglasii* strain C29. Biologisches Zentralblatt 103:495-504.

Mauthe, S., K. Bachmann, K.L. Chambers, and H.J. Price. 1985. Genetics of heterocarpy and pappus-part numbers in *Microseris douglasii* strain C28 (Asteraceae - Lactuceae). Biologisches Zentralblatt 104:1-20.

Price, H.J., K.L. Chambers, K. Bachmann, and J. Riggs. 1985. Inheritance of nuclear 2C DNA content in a cross between *Microseris douglasii* and *M. bigelovii* (Asteraceae). Biologisches Zentralblatt 104:269-276.

Chambers, K.L. 1986. The dwarf bilberry is in Oregon. Bulletin of the Native Plant Society of Oregon 19:7.

Price, H.J., K.L. Chambers, K. Bachmann, and J. Riggs. 1986. Patterns of mean nuclear DNA content in *Microseris douglasii* (Asteraceae) populations. Botanical Gazette 147:496-507.

Bachmann, K., A.W. van Heusden, K.L. Chambers, and H.J. Price. 1987. Genetic variation for the onset of flowering in *Microseris bigelovii* (Asteraceae, Lactuceae). Beiträge zur Biologie der Pflanzen 62:23-41.

Bachmann, K., A.W. van Heusden, K.L. Chambers, and H.J. Price. 1987. A second gene determining spatulate leaf tips in *Microseris bigelovii*. (Asteraceae, Lactuceae). Beiträge zur Biologie der Pflanzen 62:97-106.

Chambers, K.L. 1987. How to make a genus disappear. Bulletin of the Native Plant Society of Oregon 20:51.

Chambers, K.L. 1989. Some Oregon grasses that are "not in Hitchcock and Cronquist." Bulletin of the Native Plant Society of Oregon 22:36-37.

Chambers, K.L. 1989. Typification of *Calandrinia columbiana* Howell (Portulacaceae). Taxon 38:645-647.

Chambers, K.L. 1989. The taxonomic relationships of *Allocarya corallicarpa* (Boraginaceae). Madroño 36:280-281.

Chambers, K.L. and J. Greenleaf. 1989. *Gentiana setigera* is the correct name for *G. bisetaea* (Gentianaceae). Madroño 36:49-52.

Van Heusden, A.W., K. Bachmann, and K.L. Chambers. 1989. Variation in time and place of trichome appearance in *Microseris* hybrid J05 (*M. pygmaea* X *M. bigelovii*, Asteraceae). Biologisches Zentralblatt 108:153-161.

Bachmann, K. and K.L. Chambers. 1990. Heritable variation for heterocarpy in *Microseris bigelovii* (Asteraceae-Lactuceae). Beiträge zur Biologie der Pflanzen 65:123-146.

Bachmann, K. and K.L. Chambers. 1990. Genetic variation for the timing and site of trichomes on the leaves of *Microseris bigelovii* (Asteraceae-Lactuceae). Biologisches Zentralblatt 109:151-158.

Chambers, K.L. 1990. Rare butterfly - rare plant. Bulletin of the Native Plant Society of Oregon 23:8-9.

Chambers, K.L. 1991. The puzzle of the *Tofieldias* of Coos County. Bulletin of the Native Plant Society of Oregon 24:15-16.

Chambers, K.L. 1991. A pesty weed and a botanical joke. Bulletin of the Native Plant Society of Oregon 24:60-61.

Chambers, K.L. 1991. Thrift is both native and introduced in Oregon. Bulletin of the Native Plant Society of Oregon 24:73-75.

Chambers, K.L. 1991. Daisies will tell: How plants play the numbers game. Bulletin of the Native Plant Society of Oregon 24:84-85.

Chambers, K.L. 1991. How do you spell *Lysichiton*? Bulletin of the Native Plant Society of Oregon 24:96-97.

Chambers, K.L. 1991. Bunchberry in Oregon: *Cornus canadensis* or *Cornus unalaschkensis*? Bulletin of the Native Plant Society of Oregon 24:118-119.

Jansen, R.K., R.S. Wallace, K. Kim, and K.L. Chambers. 1991. Systematic implications of chloroplast DNA variation in the subtribe Microseridinae (Asteraceae: Lactuceae). American Journal of Botany 78:1015-1027.

Chambers, K.L. 1992. Have you ever heard of *Paxistima*? Bulletin of the Native Plant Society of Oregon 25:16.

Chambers, K.L. 1992. Learn the gender of your genera. Bulletin of the Native Plant Society of Oregon 25:30-31.

Chambers, K.L. 1992. Evolution before Darwin: The musings of Constantine Rafinesque. Kalmiopsis 2:5-9.

Chambers, K.L. 1992. Some recent taxonomic changes affecting the names of Oregon plant species. Kalmiopsis 2:16-20.

Chambers, K.L. 1992. Choosing the correct name for *Aconogonom* (*Polygonum* sect. *Aconogonom*) in Alaska. Rhodora 94:319-322.

Chambers, K.L. 1993. The grass genera of the world (a review). Plant Science Bulletin 39:36-37.

Chambers, K.L. 1993. *Agoseris*, *Claytonia*, *Microseris*, *Montia*, *Nothocalais*, *Phalacroseris*, *Stebbinsoseris*, *Uropappus*. Pages 190-193, 316-319, 320, 326, 345, 355-356, 898-900, 904 in J.C. Hickman, editor. *The Jepson Manual*. University of California Press, Berkeley.

Chambers, K.L. 1993. Some more new names for Oregon plants. Bulletin of the Native Plant Society of Oregon 26:91-92.

Chambers, K.L. 1993. *Thuja*. Pages 410-411 in Flora of North America Editorial Committee, editors. *Flora of North America North of Mexico*, vol. 2. Oxford University Press, New York.

Miller, J.M. and K.L. Chambers. 1993. Nomenclatural changes and new taxa in *Claytonia* (Portulacaceae) in western North America. Novon 3:268-273.

Battjes, J., K.L. Chambers, and K. Bachmann.1994. Evolution of microsporangium numbers in *Microseris* (Asteraceae: Lactuceae). American Journal of Botany 81:641-647.

Chambers, K.L. 1995. The contributions of Göte Turesson to plant taxonomy. Pages 37-55 in A.R. Kruckeberg, R.B. Walker, and A.E. Leviton, editors. Proceedings of the 73rd Annual Meeting of the Pacific Division AAAS on the Occasion of the 100th Anniversary of the Birth of Göte Turesson. Pacific Division AAAS, San Francisco, CA.

Chambers, K.L. 1995. What's the latest name for that plant? Oregon Flora Newsletter, vol. 1, no. 1.

Chambers, K.L. 1995. Omnia *Brodiaea* est Divisa in Partes Tres. Oregon Flora Newsletter, vol. 1, no. 3.

Chambers, K.L. 1995. More New Name Changes: Daisies and Tansies. Oregon Flora Newsletter, vol. 1, no. 4.

Chambers, K.L. 1996. A taxonomist views The Species Problem. Douglasia 20:18-19.

Chambers, K.L.1996. Notes on some interesting Oregon groundsels. Oregon Flora Newsletter, vol. 2, no. 3.

Chambers, K.L. 1996. Some observations on *Erigeron* in Oregon. Oregon Flora Newsletter, vol. 2, no. 4.

Chambers, K.L. 1997. Observations concerning the need for taxonomic research on Oregon's flora. Pages 125-132 in T.N. Kaye, A. Liston, R.M. Love, D.L. Luoma, R.J. Meinke, and M.V. Wilson, editors. Conservation and Management of Native Plants and Fungi. Native Plant Society of Oregon, Corvallis.

Chambers, K.L. and H.L. Chambers. 1997. Hedgenettles for the Oregon Flora Checklist. Oregon Flora Newsletter, vol. 3, no. 1.

Chambers, K.L. and H.L. Chambers. 1997. Key to Oregon species of *Stachys*. Oregon Flora Newsletter, vol. 3, no. 1.

Chambers, K.L. 1997. Some taxonomic notes on Oregon goldenrods, part I. Oregon Flora Newsletter, vol. 3, no. 3.

Kaye, T.N., R.J. Meinke, J. Kagan, S. Vrilakas, K.L. Chambers, P.F. Zika, and J.K. Nelson. 1997. Patterns of rarity in the Oregon flora: Implications for conservation and management. Pp. 1-10 *in* T.N. Kaye, A. Liston, R.M. Love, D.L. Luoma, R.J. Meinke, and M.V. Wilson, eds. Conservation and Management of Native Plants and Fungi. Native Plant Society of Oregon, Corvallis.

Chambers, K.L. 1998. Some taxonomic notes on Oregon goldenrods, part II. Oregon Flora Newsletter, vol. 4, no. 1.

Chambers, K.L. 1998. A new name for *Chamaesaracha* in Oregon. Oregon Flora Newsletter, vol. 4, no. 1.

Chambers, K.L. 1998. Beware of the hybrid gumplant. Oregon Flora Newsletter, vol. 4, no. 2.

Chamber, K.L. 1998. Cherchez les hommes (In *Antennaria*, boys are a minority). Oregon Flora Newsletter, vol. 4, no. 3.

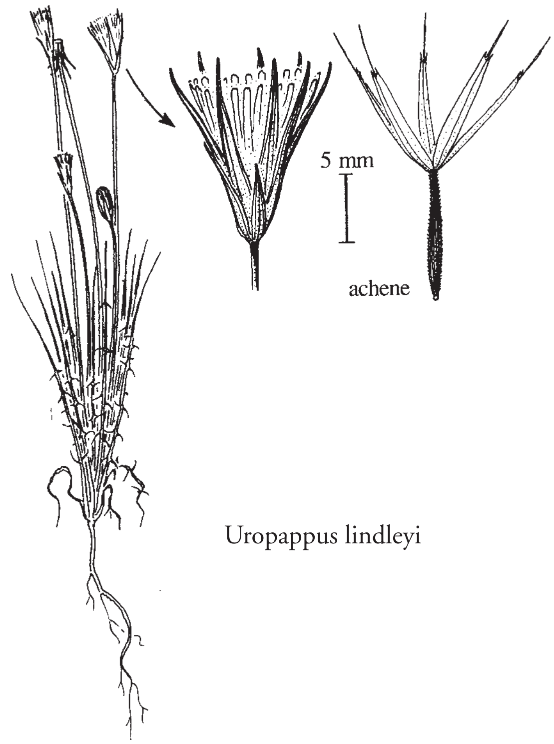
Sundberg, S. and K.L. Chambers. 1998. Checklist: Asteraceae. Oregon Flora Newsletter, vol. 4, no. 3.

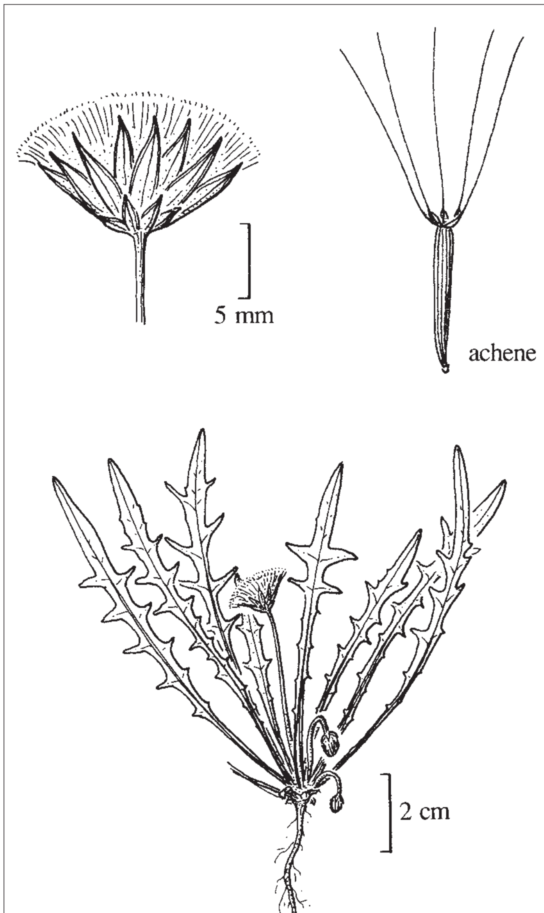
Chambers, K.L. 1999. In shooting stars, little things mean a lot. Oregon Flora Newsletter, vol. 5, no. 1.

Chambers, K.L. 1999. Some new names and clarifications for Oregon's flora. Oregon Flora Newsletter, vol. 5, no. 3.

Chambers, K.L. 2000. *Tofieldia* gives way to *Triantha* in Oregon. Oregon Flora Newsletter, vol. 6, no. 1.

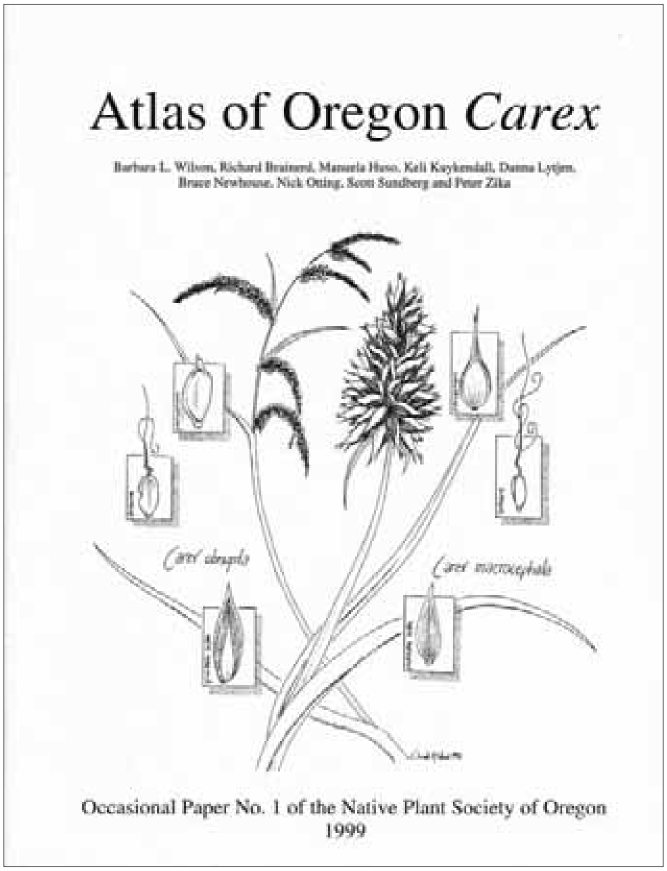
Chambers, K.L. 2000. Oregon delphiniums — easy to collect, hard to identify, part I. Oregon Flora Newsletter, vol. 6, no. 2.





Microseris elegans

Illustrations drawn for A Flora of Santa Cruz Island (Junak *et al*. 1995) by Linda Ann Vorobik.



To order either or both Occasional Papers, send check for the appropriate amount (made payable to NPSO) to: Occasional Papers, Native Plant Society of Oregon, PO Box 902, Eugene, Oregon 97440-0902.

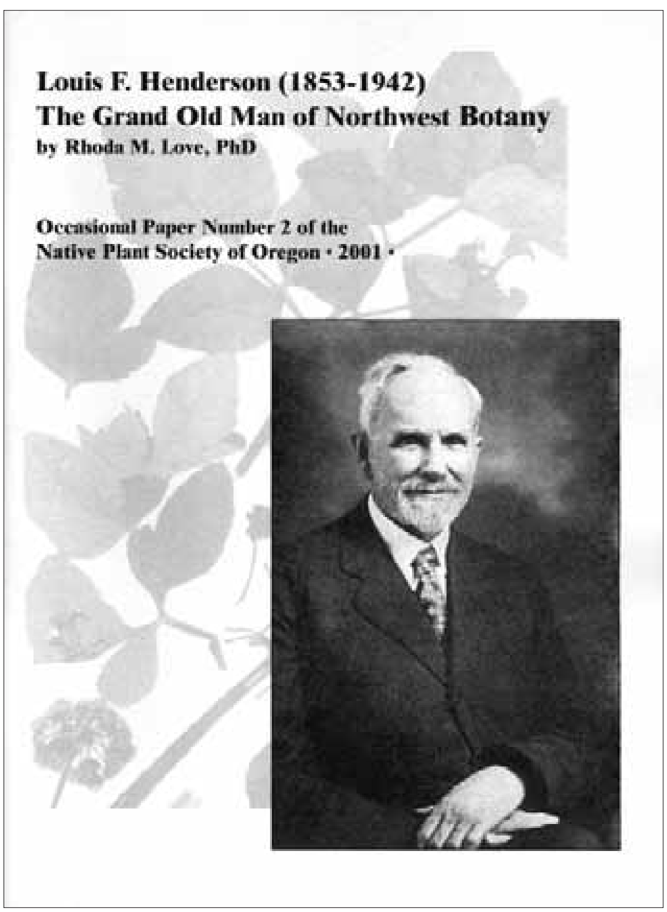
Atlas of Oregon Carex

Rich with information, a distillation of many decades of herbarium records and sightings by Oregon botanists. Contains 128 location maps, one for each Carex taxon in Oregon. Also included are a synonymy, fun facts about sedges, a history of the project, and Oregon geography maps. 29 pages.

Authors: Barbara L. Wilson, Richard Brainerd, Manuela Huso, Keli Kuykendall, Danna Lytjen, Bruce Newhouse, Nick Otting, Scott Sundberg, and Peter Zika.

Publication Date: May 1999. **Price: $5.**

"Everyone who is serious enough about botany to go beyond colorful wildflowers and appreciate the beauty of sedges should have a copy of this Atlas. By providing distribution maps and species lists, it narrows the field of possibilities and serves as a great companion to *Carex* identification keys."—Cindy Roché.



Louis F. Henderson (1853-1942)
The Grand Old Man of Northwest Botany

Botanist Louis Henderson was a larger-than-life figure in the mold of John Muir. Possessed of great physical strength and stamina, he energetically explored the mountains, deserts, forests, and seacoasts of the Northwest for 65 years, adding greatly to our knowledge of the flora. LFH was also a writer, raconteur, and mountain climber, as well as a conscientious family man.

This fascinating, peer-reviewed, 64-page biography includes 56 historic and modern images. It is carefully and exhaustively researched with 133 notes plus chronology, lists of publications, and plants named for Henderson.

Author: Rhoda M. Love, PhD

Publication Date: January 2001 **Price: $10.**

"A significant landmark in the documentation of botanical history of the Pacific Northwest"—David H. Wagner, former Curator, University of Oregon Herbarium.

"I was totally delighted with the Henderson biography. I found myself envying the wonderful passion of your endeavor to bring this botanist to light."—Catherine Hovanic, Washington Native Plant Society.