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Source: *Contributions from the Gray Herbarium of Harvard University*, 1957, No. 183 (1957), pp. 1-149, 151

Published by: Harvard University Herbaria

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**CONTRIBUTIONS FROM THE GRAY HERBARIUM
OF HARVARD UNIVERSITY**

Edited by

Reed C. Rollins and Robert C. Foster

NO. CLXXXIII

**THE SYSTEMATICS AND EVOLUTION
OF TOWNSENDIA (COMPOSITAE)**

By

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PUBLISHED BY

**THE GRAY HERBARIUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASS., U.S.A.**

Issued 31 Oct., 1957

ABSTRACT

The genus *Townsendia* (tribe *Astereae*) consists of perennial, biennial, and annual herbs that occur in the western United States, Mexico, and southwestern Canada. Twenty-one species are now recognized in the genus; two new species and one new variety have been described in this paper.

Reproduction in several species of the genus has received cytogenetic and embryological study. Meiosis in both micro- and megasporogenesis in diploid, sexual plants ($n = 9$) is regular with the formation of tetrads of micro- and megaspores. At anthesis the pollen grains are 3-nucleate, and the percentage of aborted grains is very low. Development of the female gametophyte from the megasporule tetrad is sometimes trisporic and sometimes tetrasporic. The mature female gametophyte in sexual plants usually consists of from 12 to 16 nuclei. Apomixis has been detected in 12 species. Meiosis in both micro- and megasporogenesis in polyploid, apomictic plants ($2n = 27-36$) is irregular with many or all of the chromosomes occurring as univalents at metaphase I. When some bivalents are present in microsporogenesis, a tetrad usually is produced, but a wall often encloses the whole tetrad, and a giant, several-nucleate pollen grain results; at anthesis the percentage of aborted grains is high. When no bivalents are present in microsporogenesis, a restitution nucleus (chromosome clump) is formed at metaphase I; the following anaphase is equivalent to anaphase II of normal meiosis, and a dyad with unreduced nuclei results. The two halves of the dyad develop separately into 3-nucleate pollen grains that are conspicuously larger than those produced by diploid, sexual plants; at anthesis the percentage of aborted grains is high. It is suggested that the unreduced dyads resulting after apomictic megasporogenesis are produced in the same manner as those in apomictic microsporogenesis. The megasporule dyad develops directly into a 2-nucleate embryo sac, and after two series of mitotic divisions the female gametophyte in apomictic plants matures at the 8-nucleate level. Division of the unreduced egg nucleus is initiated slightly before that of the two fused polar nuclei. The female gametophyte escapes reduction by diplospory; apomixis is obligate, and pollination is not required to initiate development of the embryo or endosperm. No diploid plants are known to be apomictic; similarly, no polyploid plants are known to be sexual.

The apomicts have not been given special taxonomic recognition. They have been referred to species known also from one or more sexual populations. Apomictic plants are concentrated at the higher elevations and higher latitudes relative to the whole range of the species in which they occur. Apomixis is found most commonly in species with the perennial habit; however, it occurs also in some biennials.

Hybridization apparently has been extensive in the genus. Intermediate populations involving 15 species have been found. Certain apomictic races in six species exhibit morphological evidence of hybridity, but other apomicts are clearly of non-hybrid origin.

The species of *Townsendia* are considered to be mostly of recent derivation. The most primitive species, *T. formosa*, has many characters in common with three other genera, *Dichaetophora*, *Astranthium*, and *Boltonia*. Geographic isolation may have been the principal factor governing speciation in *Townsendia*. Experimental crosses and putative natural hybrids suggest that genetic isolating barriers are not involved in initial evolutionary

divergence. Polyploidy apparently has not been a mechanism of evolution, as it seems to be closely associated with obligate apomixis. Several examples of parallel or convergent evolution have been discussed.

INTRODUCTION

A cytotaxonomic study begun with several seed collections was the forerunner of the present paper. Early in the study it became evident that apomixis might be present in *Townsendia*. In the limited herbarium material then examined, several of the specimens seemed difficult to determine. Thus, it appeared that *Townsendia* was deserving of a full-scale systematic investigation, even though it had been revised by Larsen (1927).

From several standpoints *Townsendia* has proved to be an ideal genus in which to employ some of the more recently developed taxonomic techniques. The western North American distribution of its 21 species offers certain practical advantages for a biosystematic investigation. Field studies within the ranges of all the species have been made. Some of these have been necessarily brief, but the plants are within a convenient distance for further population studies of a more detailed nature. The concentration of herbarium material of *Townsendia* is in American herbaria and a large percentage of this has been examined. With the recent interest in collecting in the western United States, most of the species have become well represented by herbarium specimens. A knowledge of intraspecific variation is therefore possible, and, where feasible in the present systematic treatment, an attempt has been made to note the type of population diversity that has been encountered. The small size of the plants of most of the species frequently has permitted collectors to include several plants on a single herbarium sheet. Some herbarium specimens approach being "mass" collections. Abundant plants in single collections have facilitated the understanding of intra-population variation.

The position of *Townsendia* in the *Astereae* is a fortunate one from the comparative cytological standpoint. Relatively few investigations of a cytological nature have been made in this tribe of the *Compositae*. *Erigeron* and *Aster* are the only genera of the tribe other than *Townsendia* that have received more than cursory cytological attention, while genera in some of the other tribes of the *Compositae*, especially in the *Cichorieae*, have been the subjects of considerable cytotaxonomic and cytogenetic interest. The chromosomes of *Townsendia* are large and easily prepared for observation. Although chromosome morphology has proved of

little systematic or evolutionary interest in the present study, more intensive future investigations may reveal its importance.

As an experimental subject, *Townsendia* may have potentialities which are now completely unexploited. However, it will probably be necessary to grow most of the species under outdoor conditions in the western portion of the United States. Few of the species exhibit entirely normal growth in the greenhouse or in the garden at Cambridge, Massachusetts. But in the garden at Pullman, Washington and probably in other areas of the West with continuously cold winters and slightly basic soils, entirely satisfactory growth of the plants may be obtained.

Most of the species appear not to have strong genetic isolating mechanisms. However, growing hybrids to more than the first or second filial generations may show up isolating barriers of the genetic type which are not expressed in first-generation hybrids. If it were possible to demonstrate why species which appear to be cross-compatible with other species can maintain clear or only slightly blurred specific boundaries when they grow side by side, information on a problem of wide biological significance would be obtained. The possibility for such a study is present in *Townsendia*.

In *Townsendia*, studies on the evolutionary significance of polyploidy appear to have little promise because of the strong correlation of polyploidy with obligate apomixis. However, the opportunities in *Townsendia* for research on the causal aspects of polyploidy and apomixis have not been exhausted.

The present investigation embodies an attempt to bring together as much information about *Townsendia* as is now available. It is hoped that the systematic treatment will provide a solid foundation upon which future investigations may be built. Obviously, all of the problems associated with *Townsendia* have not been solved. But if this study can serve as a reference point from which problems in plant migration, population variability, and phylogenetic modification can be attacked, then a primary aim will have been fulfilled.

ACKNOWLEDGMENTS

The inspiration from Dr. Reed C. Rollins has contributed much to this study. He provided numerous suggestions and facts which aided in the research and writing of the paper, and his help in obtaining funds, facilities, and material for the investigation has been invaluable. Appreciation is extended also to Dr. Marion Ownbey for his advice when the study was in its early stages.

I wish to thank the curators of the herbaria from which specimens have been used. These herbaria are listed at the beginning of the systematic treatment.

Most of the field investigations were financed by a generous grant from the Fernald Fund of Harvard University. To Mr. F. W. Hunnewell of Wellesley, Massachusetts, a large measure of appreciation is due for providing the Fernald Fund. I am indebted to Mr. Irwin Lane and Mr. Henry Andreozzi for handling the collections of living plants which were sent to them while the field studies were in progress.

A grant from Sigma Xi has helped cover the expense of the illustrations.

Dr. R. E. Schultes and Dr. R. C. Foster have edited the Latin diagnoses and Mrs. L. Schwarten has given assistance in the library.

Dr. S. J. Preece provided fixed material from the experimental garden at the State College of Washington which has formed an important part of the embryological investigations. The assistance in the field studies given by Dr. Preece in 1952 is also gratefully acknowledged.

Seed collections have been received from Mr. J. T. Howell, Dr. Quentin Jones, Dr. Marion Ownbey, Dr. C. L. Porter, and Dr. B. L. Turner. I am indebted to Dr. W. A. Weber for guiding me to an alpine habitat of the rare *Townsendia Rothrockii*. Mr. and Mrs. W. L. Bartholomew have provided detailed field notes and abundant seed and herbarium material of the species of *Townsendia* in the Uinta Basin of Utah.

Dr. R. B. Channell, Mr. E. Hernandez X., and Mr. D. R. Whitehead gave much-needed help with the multitude of details which were attended to in the final preparatory stages of the paper.

The devoted assistance of my sister, Mary Lou Beaman, in the summer of 1956 made possible a timely completion of the study.

HISTORICAL ACCOUNT

Some details in the history of the genus *Townsendia* have been recorded in the revision by Larsen (1927). In addition to two new species in the present treatment, three species (*T. dejecta*, *T. minima*, and *T. anomala*) have been described since the time of Larsen's treatment. One of these, *T. minima*, is recognized as *T. montana* var. *minima* in this study. The other two are placed in synonymy.

Botanists who have done the most work with *Townsendia* have generally considered the genus a difficult one. Thus Gray (1880) stated: "Ever since the discovery of a considerable number of species, this very characteristic genus of the Rocky Mountain region has been particularly difficult." And Marcus Jones (1893) in his Notes on *Townsendia* stated: "This genus has always been

a trying one to me because the descriptions have not fitted the plants as they grow." Heiser (1948) noted that "A number of problems in the genus *Townsendia* call for extensive field work and experimental studies." The recognition of apomixis and its effects in the genus has been a great aid in solving problems which confronted and to some extent confounded previous investigators.

The taxonomic treatment of the present paper corresponds more closely to that by Gray than to the revision of Larsen. Improvements on Gray's treatment have been possible mainly because many more specimens are now available. The present study indicates that only three of the 17 species recognized by Gray cannot be maintained. Generally, the varieties he described are not recognized in this treatment, but one of his varieties, *T. sericea* var. *leptotes*, was elevated to specific rank by Osterhout and is here recognized as such. The revision by Larsen, although based on more specimens than were available to Gray, shows a lack of understanding of *Townsendia*. Larsen's confusion of *T. mensana* with *T. Hookeri* (*T. sericea* in her treatment), of *T. condensata* with *T. spathulata*, and of *T. Fendleri* and *T. annua* with *T. strigosa* has caused considerable difficulty for botanists working with the flora of the western United States. Furthermore, her key is not satisfactory for determining many of the species.

One helpful contribution of Larsen's (1927) study of *Townsendia* was her demonstration that Hooker's "species," *T. sericea*, was based on two specifically distinct elements. She indicated that plants collected in the "Rocky Mountains" by Drummond accord with Hooker's description of *T. sericea* in his "Flora Boreali-Americana," and that those collected by Richardson (which are the type of *Aster*? *exscapus* = *T. exscapa* [Richards.] Porter) present some discrepancies with Hooker's description, particularly in the character of the leaf, pubescence, and pappus. She consequently interpreted the Drummond plants as the type of *T. sericea* Hook. and the type of the genus.

Two specifically distinct elements were represented in the plants collected by Richardson and Drummond. However, *T. exscapa* must be taken as the type of the genus because its type was included in the original species of *Townsendia*. Furthermore, Hooker's species, *T. sericea*, cannot be maintained to include the element of the original material which is not *T. exscapa* because it included the type of the earlier *Aster*? *exscapus*. This other element is referred to a newly described species, *T. Hookeri*.

THE LOCALITIES OF NUTTALL'S TOWNSENDIA COLLECTIONS

The largest number of species recognized in this study which has been described by a single botanist is four. Both Asa Gray and Thomas Nuttall described that number. The specimens upon which Gray's species are based were obtained by several collectors and their data are fairly precise. The specimens upon which Nuttall's species are based were collected by himself during his journey with the Wyeth expedition from St. Louis, Missouri, to Fort Vancouver, Oregon, in 1834. In general the localities Nuttall listed for his specimens are almost impossibly vague. The localities for his specimens of *Townsendia* are no exception. No journal made by Nuttall during this trip is known (Graustein, 1951), so most of the information about his localities must come from his published account (1840, 1841) and the label data on his specimens.

In addition to the papers of Jepson (1934) and Pennell (1936) which consider Nuttall's journey across the West, the problem has recently been approached by Goodman (1943), Barneby (1947), and Rollins (1950) in regard to *Parthenium alpinum*. One of the species of *Townsendia* which Nuttall described (*T. spathulata*) has range limitations somewhat similar to *Parthenium alpinum*. The other species of *Townsendia* which Nuttall described also have relatively small and well-defined ranges. Therefore, it has been considered worthwhile to bring together the available data on Nuttall's *Townsendia* collections and make a critical analysis of them. For recording the label information on the specimens in the British Museum, I am indebted to Dr. Rollins.

The four species Nuttall described and the one additional species he collected are listed below with the data which Nuttall published and the data which accompany his specimens.

Townsendia grandiflora.

Published locality: "Hab. With the preceding, . . ." [the preceding is *T. strigosa*].

Label localities: Hills of the Platte and into the R. Mts. (BM). Black Hills of the Platte (BM). Plains of Platte, June (PH). Platte (GH, ex Herb. John A. Lowell). Platte (NY, not in Nuttall's handwriting). Platte, Hills (GH, in Gray's handwriting). Plains of the Platte (GH, in Gray's handwriting).

Townsendia Hookeri Beaman (the determination by Nuttall was *T. sericea* Hook.).

Published locality: "Hab. On the Black Hills, (an alpine chain

toward the sources of the Platte). Flowering probably in April." None of Nuttall's collection of this species is in American herbaria and through an oversight of mine the data of the specimen in the British Museum were not recorded by Dr. Rollins.

Townsendia incana.

Published locality: "Hab. With the above [*T. Hookeri*]. Flowering in June."

Label localities: Black Hills of the Platte, June (BM). Black Hills of the Platte, grassy plains (BM). Black Hills of the Platte (PH). Platte plains (GH, ex Herb. John A. Lowell). Rocky Mts. lat. 42° (GH, in Gray's handwriting).

Townsendia spathulata.

Published locality: "Hab. With the above." [*T. Hookeri* and *T. incana*].

Label localities: Black Hills of the Platte, June (BM). Black Hills of the Platte in "[?, nearly illegible] campis etato rocky" (BM). Black Hills of Platte (PH). Black Hills [of, illegible] Platte (GH, ex Elias Durand).

Townsendia strigosa.

Published locality: "Hab. On the Black Hills, (or eastern chain of the Rocky Mountains,) near the banks of the Platte.—Flowering in June."

Label localities: Black Hills of the Platte (BM). Black Hills of the Platte, June (BM). Black Hills (GH, in Gray's handwriting). R. Mts. Platte (PH).

The most confused and inconsistent of the sets of data above is associated with *T. grandiflora*. It seems unlikely that Nuttall could have collected *T. strigosa* and *T. grandiflora* together as he stated. The well-defined ranges of the two species are not known to be less than 100 miles apart at their closest points. *Townsendia grandiflora* is probably the eastern-most species of the genus collected by Nuttall. It appears likely that the locality "Plains of Platte" as is on the Philadelphia Academy specimen is more accurate than the published locality or that on the specimens of the British Museum. It is possible that Nuttall obtained the species more than once, which may account for some of the diversity of his label information. Evidence is presented in the systematic treatment under the discussion of *T. spathulata* which suggests that Nuttall obtained this species from more than one locality.

Nuttall's inference that he obtained *T. Hookeri*, *T. incana*, and *T. spathulata* together seems likely. I have obtained these

three species from a single locality near Alcova, Natrona County, Wyoming (*T. Hookeri*, Beaman 877, *T. incana*, Beaman 875, and *T. spathulata*, Beaman 878). *Townsendia incana* and *T. spathulata* have been obtained at this locality by other collectors also. It is interesting that *Parthenium alpinum* has recently been obtained by Ripley and Barneby and by Porter at this same locality after being known only from the type collection for more than 100 years. Ironically, Nuttall's locality data for *Parthenium* and those for the *Townsendia* species are entirely different.

It seems probable that Nuttall's term "Black Hills of the Platte" embraces a rather large area in central and western Wyoming. His "Black Hills" are possibly the Wind River Mountains. These mountains are an alpine chain and are at one source of the Platte (actually Sweetwater) River. They would have been the highest mountains which Nuttall saw in Wyoming, as he followed the Oregon Trail. Aside from his *Townsendia* collections, the "Black Hills" locality was not frequently used by Nuttall. He used it for *Gnaphalium dimorphum* (= *Antennaria dimorpha*), for *Antennaria plantaginea* (= ?, I have not seen specimens of this Nuttall collection), and for *A. parvifolia*. Neither *Antennaria dimorpha* nor *A. parvifolia* has a very limited range as do the *Townsendia* species, and therefore are of little value for locating the "Black Hills." One feature about Nuttall's locality data throughout his paper (1840, 1841) is that he frequently used the same or similar locality information for each species or most of the species of a genus. This makes one wonder if the similarity always resulted from a coincidence of collecting several species of a genus in one locality, or if some other factor accounts for the similarity. In *Townsendia*, with the possible exception of *T. grandiflora*, Nuttall's locality data are vague enough to escape being classed as incorrect.

GEOGRAPHICAL DISTRIBUTION, CLIMATIC AND EDAPHIC REQUIREMENTS

Townsendia is primarily a genus of the Rocky Mountains of the United States. The ranges of apomictic populations of three species extend into Canada. One of these species, *T. exscapa*, is found also in Mexico. Only one other species, a Mexican endemic, is now known from that country. The easternmost range of a member of the genus is that of *T. exscapa*, which occurs as far east on the Great Plains as northeastern Nebraska. The western limit of the genus is on the Columbia River plateau in central

Oregon where *T. florifer* occurs. *Townsendia* is mostly found above 3500 to 4000 ft., but along the Columbia River in Oregon and Washington *T. florifer* is at less than 1000 ft. The upper elevational limit of the genus is marked by apomictic populations of *T. Rothrockii* and *T. leptotes* which occur at least as high as 13,000 ft. in Colorado.

Ten species have been collected in both Colorado and Wyoming; nine occur in Utah and seven are found in New Mexico. Idaho and Nevada each have six; Montana has five, and Arizona has four species. Several of the western states have two or three species each. It is unusual for a species of *Townsendia* to be found in more than four states, and ten of the 21 species occupy only small areas in one or two states. Narrow endemism may be regarded as a common feature of the genus.

It may be inferred from the distributions outlined above that both latitudinal and altitudinal climatic influences are important in governing the distribution of the species of *Townsendia*. *Townsendia exscapa*, *T. Hookeri*, and *T. leptotes* are the only species which do not occur within a relatively narrow climatic province. Even in the latter two of these species, the sexual forms are restricted to small areas with nearly uniform climatic conditions. Thus it seems probable that climate has had an important role in the evolution of the members of the genus.

In many instances edaphic factors appear to be even more important than climatic factors in regulating the distribution of the species of *Townsendia*. Especially within the range of a species, the occurrence of plants on very localized edaphic situations is frequently striking. As a generalization, with not too many exceptions, it may be stated that the acaulescent, rosulate forms require more highly specialized edaphic situations than do the caulescent types. The former mostly require open, finely divided limestone, sandstone, or shale rubble with a sparse vegetation. Edaphic sites of this type are illustrated by the habitat photographs in Plate XV, figs. 1 and 2 and in Plate XVI, fig. 2. These edaphic conditions might be characterized as stable in a short-time sense and unstable in a longer- (geological) time sense. Even though the caulescent forms are less strictly limited edaphically, their requirements are somewhat parallel to those of the acaulescent types.

Soil samples have been collected at habitats of all the species, but time limitations have not permitted an analysis of these. A pH analysis is planned as a future study. Tentatively it may be inferred from the general character of the soils of the western

United States that the species in the more arid habitats occur in soils on the basic side of the pH range, while those in the moister habitats are probably in neutral or only slightly acid soils.

GENERIC RELATIONSHIPS

In a genus with species as closely related to one another as are those of *Townsendia*, it would seem that relationships of the genus to other genera might also be evident. However, few investigators have committed themselves on the generic relationships of *Townsendia*. The limits of the genus never have been questioned. There has been but a single species placed in *Townsendia* which belongs in a different genus, and this was first excluded by Gray, its author. Likewise, there have been no species transferred from other genera into *Townsendia* (with the exceptions of *T. exscapa* and *T. florifer* which were described originally with doubt as to their generic position). Consequently, the generic relatives of *Townsendia* are not revealed by its nomenclatorial history.

The genera conventionally assigned close to *Townsendia* have not had a similarly tranquil history. The many changes in *Aster* are well known. *Astranthium* has been with *Bellis*; *Dichaetophora* has been with *Boltonia*; and *Keerlia* is now in *Chaetopappa*. These examples by no means exhaust the list of changes, but the reader is referred to Shinners (1946a) for further details.

Although the uncomplicated nomenclatorial history of *Townsendia* suggests for it a distinct phyletic position, its features were not considered unique by Bentham (1873). In his comprehensive "Notes on the Compositae" he wrote (p. 408): "Thus we have the Asiatic and North-American *Boltonia*, the Asiatic *Heteropappus*, and the N.-American *Townsendia*, *Monoptilon*, and *Psilactis* differing from the typical *Asters* of the same regions in scarcely any thing but the pappus." Gray (1888) in his "Synoptical Flora" in the section *Megalastrum* of *Aster* tersely wrote: "related to subsection *Xylorrhiza* and to *Townsendia*." And Larsen (1927) noted that "the heads [of *Townsendia*] resemble those of the closely related genus *Aster*." Otherwise, ideas of the generic relationship of *Townsendia* have been indicated only by its systematic position in works by such authors as Gray (1888) and Hoffmann (1897). The rationale of the statement by Gray (quoted above) is evident. Section *Megalastrum* includes *Aster Wrightii* which Gray had once put in *Townsendia*. From the present study, it appears that *Aster Wrightii* could be considered to have

only a rather distant relationship with *Townsendia*. Species of several other genera have a considerably closer relationship.

In Shinners' (1946b) study of some of the *Astereae* he noted that in the American genera of the heterochromous *Astereae* an arrangement on the basis of the form of the receptacle was better than that based on the pappus. Those conical-receptacled genera which he treated are *Egletes*, *Erigeron* (in part), *Aphanostephus*, *Astranthium*, *Dichaetophora*, and *Boltonia*. In his key to separate the above genera, *Astranthium*, *Dichaetophora*, and *Boltonia* fall into one group. An examination I have made of these three genera indicates that they have a number of morphological similarities. Also, they have characteristics in common with *Townsendia*, which was not included in Shinners' treatment because it was not at that time known to have a conical receptacle. In the present study, *Townsendia formosa* has been found to have a conical receptacle. Through this species it is possible to recognize the relationship of *Townsendia* with *Dichaetophora*, *Astranthium*, and *Boltonia*. Another feature which indicates their relationship is the stem pubescence, which is consistently of simple, strigose trichomes. The leaves, especially of *Dichaetophora* and some of the *Astranthium* species, are very similar in shape, texture, and pubescence to those of *T. formosa*. The pappus of *T. formosa* is very similar to that of *Astranthium*, while the pappus of *Boltonia* and *Dichaetophora* is somewhat similar to that of *T. eximia*. The achenes, which are compressed, ovate in shape, and with two conspicuous margins (extended into wings in *Dichaetophora*), are very similar in all four genera. *Dichaetophora* also has duplex, glochidiate achenial hairs ("peculiar gland-tipped hairs" according to Shinners) on the central portion and margins of the achenes. These hairs are indistinguishable from those of several species of *Townsendia*. The achenes of *Dichaetophora* also are papillose in a manner very similar to those of some of the members of *Townsendia*.

The four genera also have a close phytogeographic relationship. The center of diversity of *Townsendia* is in the southern cordillera of the United States. The centers of *Dichaetophora* and *Astranthium* are not far to the south, and that of *Boltonia* is to the east.

Townsendia and *Dichaetophora* are probably the two closest members of this four-genus alliance, but *Astranthium* is not too distantly related. *Boltonia* seems somewhat more widely set apart.

Within *Townsendia*, the characters I regard as primitive are:

a perennial, fibrous-rooted, rhizomatous and stoloniferous habit; erect, monocephalous stems; large, thin, glabrate, spatulate leaves; lightly pubescent stems; large heads; a conical receptacle; several rows of broad phyllaries with narrowly scarious and minutely ciliate margins; large, obovate achenes; and a small, unelaborated pappus. With the exception of the phyllaries, about which I am not sure, these characters may be considered to be primitive (when present) also in the three other genera under discussion. *Townsendia formosa* appears to be a more unspecialized form than the other *Townsendia* species, and also the members of the other three genera.

The concept of a small, squamellate, unelaborated pappus as a primitive character requires explanation. Under most circumstances it would be looked upon as a reduced feature. But in this case, *T. formosa* and three closely related genera have the small pappus. Within *Townsendia*, the species most closely related to *T. formosa* (*T. eximia*) has a larger but similar pappus. The derived relatives of *T. eximia* in turn have a pappus which is even more highly elaborated. It seems, therefore, that the evolutionary trend has been in the elaboration rather than the reduction of the pappus. The selective advantage of a large pappus as an agent of dispersal seems evident.

The alternative explanation, that the pappus of *Townsendia formosa* is a reduced feature, would require the postulate that the genera related to *Townsendia* have been more recently segregated from *T. formosa* stock than have the rest of the *Townsendia* species. This explanation seems improbable. Although many similarities between *T. formosa* and the three other genera have been indicated above, the latter still have greater differences from *T. formosa* than do the other species of *Townsendia*. For example, *Dichaetophora*, which seems to be the genus most closely related to *Townsendia*, is comprised of a single annual species. This life-form is surely a long phylogenetic distance from the rhizomatous, long-lived *T. formosa*.

It is beyond the scope of the present work to consider the position of *Townsendia* and its close generic relatives in regard to their position with the rest of the *Astereae*. However, it should be noted that the embryological similarities between *Townsendia* and *Erigeron* (considered in the section on reproduction) do not necessarily suggest a close relationship for the two genera. These peculiar embryological features may eventually be found in still other members of the *Astereae*.

SPECIES CONCEPT

It is hoped that the present systematic treatment approaches an ideal which has been expressed by Cain (1944). He stated (p. 7): "Taxonomy attains a logical basis when the data of comparative morphology can be arranged in a geographical pattern that coincides with the probable phylogeny of the group and the history of the floras . . . in which it has been involved." In this study an attempt has been made to designate the taxa by a system which applies insofar as possible a traditional nomenclature, yet emphasizes the morphologically recognizable units on a geographic basis.

There is a marked tendency in *Townsendia* for species with the same flowering periods to have allopatric ranges. A criterion of strict genetic isolation cannot be used in *Townsendia*. Such an approach would result in the "lumping" of most or all of the species into one. Geographic barriers are most important in isolating the species of *Townsendia*. If genetic barriers do exist in the genus, they are probably not strongly expressed in the first hybrid generation in most instances.

An understanding of the mechanism of reproduction in *Townsendia* has been a necessary basis for explaining peculiarities of geographic distribution of some of the species. Cytogenetic and embryological data have therefore been of value in facilitating an understanding of the comparative morphology of the group on a geographic basis. But these data have been of little value in the determination of specific boundaries.

Most of the species are nearly parallel in their degree of distinctness. However, *T. formosa* possesses a considerably larger set of unique characteristics than does any other species. Those taxa at the varietal level were placed there as geographic segregants with fewer characters distinguishing them from their nearest relatives than were usually available to distinguish species. No complete intergrading series is known between the varieties, in the two species where they were designated. The term "variety" rather than the term "subspecies" is used for the infraspecific units primarily because its use in this sense has long been accepted in botanical classification. According to the International Code of Botanical Nomenclature (Lanjouw et al., 1956, Article 4) either of the terms might have been used. In the present taxonomic interpretation of *Townsendia*, it would not have been possible to use both of these infraspecific categories.

REPRODUCTION

Apomixis in *Townsendia* previously was suggested by five indirect lines of evidence reported in a preliminary cytogenetic investigation in the genus (Beaman, 1954). In the present study the problem of apomixis was attacked directly by comparative embryological examinations of mega- and microsporogenesis and subsequent development in sexual and apomictic populations. Knowledge of the mechanism of apomixis in *Townsendia* has been considered indispensable to a formulation of taxonomic concepts in the genus. Different types of apomixis may have different effects on evolutionary trends. For example, pseudogamous apomicts are more dependent on environmental factors, such as pollinating agents, than are autogamous apomicts. Facultative apomicts may lack some of the efficiency in reproduction which characterizes obligate apomicts. But obligate apomicts may be less plastic under the action of selective forces than are facultative apomicts. Therefore, this study was designed to expose the morphological and cytological features of apomixis in *Townsendia* and to evaluate the significance of apomixis to evolution in the genus.

MATERIALS AND METHODS

The plant material which has been used in this study is listed in Table 1. Voucher specimens are filed in either the Gray Herbarium of Harvard University or in the Herbarium of the State College of Washington. The plants were grown in the experimental gardens at Harvard University in Cambridge, Massachusetts or at the State College of Washington in Pullman, Washington. In some cases buds used in the study were taken from plants growing in their native habitat.

Studies of microsporogenesis and male gametophyte development were made from florets fixed and smeared according to a method previously outlined (Beaman, 1954). A few observations of microsporogenesis were made in embedded and sectioned anthers prepared along with the florets used in the study of megasporogenesis. However, this material was unsatisfactory for critical examinations.

Studies of pollen were made from unopened (*i.e.*, pre-anthesis) florets from herbarium specimens. The corollas of these florets were macerated in a drop of aceto-carmine on a slide and observed immediately under the microscope. Pollen size and

degree of abortion are readily apparent by the use of this rapid technique, which was employed in the taxonomic study to determine whether the herbarium specimens represented sexual or apomictic populations. The pollen nuclei become darkly stained after being exposed to aceto-carmine for from one to ten minutes. Pollen may be satisfactorily photographed for about 45 minutes after being placed in aceto-carmine. If the staining period is longer, the cytoplasm becomes darkly stained, and a satisfactory contrast between the nuclei and the cytoplasm cannot be obtained.

Studies of megasporogenesis, female gametophyte development, and embryogeny were made from buds fixed either in Belling's modified Navashin's fluid or in a Carnoy's fluid (6 parts absolute alcohol: 3 parts chloroform: 1 part glacial acetic acid). When Carnoy's fluid was used, the buds were transferred to 70 per cent alcohol after being in the fixative for about one hour. With Navashin's fluid, aspiration was sometimes employed. The best fixation was obtained by removal of the top portion of the achene before fixation. Aspiration was unnecessary when ovaries were opened in this manner. The period of fixation lasted from a few days to over two years. As might be expected, the material used shortly after fixation yielded the best results. Also, material fixed in Navashin's fluid gave much better results with the paraffin-embedded technique than did that fixed in Carnoy's fluid. Material fixed in the latter was used only to supplement the material fixed in Navashin's fluid.

Material fixed in Navashin's fluid was washed in water and dehydrated in a tertiary butyl alcohol series. Material fixed in Carnoy's fluid was transferred directly from 70 per cent alcohol to the tertiary butyl alcohol series. The material was embedded in Fisher Tissuemat and sectioned at from 10 to 15 microns. Even in old florets, 10 microns proved to be the most satisfying thickness. A ferric ammonium sulphate-haematoxylin staining schedule, described by Esau (1944), gave good results. The slide preparations are in the personal collection of the author.

The photomicrographs were made with Bausch and Lomb photomicrographic equipment and a Zeiss microscope with apochromatic 20X, 40X, and 90X objectives. Ansco Isopan film was used.

THE MALE REPRODUCTIVE PHASE

In a previous paper (Beaman, 1954) studies of microsporogenesis in ten species (13 according to the species delimitations

then used) of *Townsendia* were reported. At that time the basic chromosome number $x = 9$ was postulated for the genus. In diploid, sexual plants almost no meiotic irregularities were found, but a high degree of meiotic irregularity was encountered in polyploid, apomictic plants. The specific names of some of the material used in the previous study (l.c.) should be emended as follows: *T. anomala* (culture 33) = *T. condensata*; *T. arizonica* (cultures 4 and 5) = *T. incana*; *T. Hookeri* (culture 38) was

TABLE I.
Material of *Townsendia* used in the embryological
and cytological investigations.^{1,2}

Taxon	Collection	Culture	2n	Place grown	Date of fixation
			Chromosome number		
<i>T. condensata</i>	Beaman 893	—	?	Native habitat	Aug. 1954
<i>T. condensata</i>	Witt 1845	47	ca. 36	Pullman, Wn.	Spring 1955
<i>T. eximia</i>	Beaman 699	699	18	Native habitat and Cambridge, Mass.	June 1954 Nov. 1955
<i>T. eximia</i>	Beaman 704	—	18	Native habitat	June 1954
<i>T. eximia</i>	Beaman 719	—	18	Native habitat	June 1954
<i>T. eximia</i>	Beaman 740	—	18 & 20	Native habitat	June 1954
<i>T. eximia</i>	Beaman 745	—	18	Native habitat	July 1954
<i>T. formosa</i>	Beaman 994	994	18	Cambridge, Mass.	June 1956
<i>T. glabella</i>	Beaman 761	761	18	Cambridge, Mass.	June 1956
<i>T. grandiflora</i>	Beaman & Preece 509	39	18	Pullman, Wn.	Spring 1955
<i>T. grandiflora</i>	Beaman 744	—	18	Native habitat	July 1954
<i>T. incana</i>	Preece & Turner 2617	5	18	Pullman, Wn.	Spring 1953
<i>T. incana</i>	Beaman 802	802	18	Native habitat	July 1954
<i>T. incana</i>	Beaman 971	971	18	Cambridge, Mass.	Nov. 1955
<i>T. incana</i>	Preece & Turner 2975	6	ca. 27 (variable)	Cambridge, Mass. and Pullman, Wn.	Nov. 1955 Spring 1955
<i>T. incana</i>	Preece & Turner 2510	17	ca. 30	Pullman, Wn.	Springs of 1953 & 1955
<i>T. incana</i>	Beaman 801	—	29	Native habitat	July 1954
<i>T. incana</i>	Beaman 875	875	36	Native habitat	Aug. 1954
<i>T. mexicana</i>	Beaman 1002	—	18	Native habitat	Sept. 1954
<i>T. montana</i> var. <i>montana</i>	Beaman & Preece 505	35	18	Pullman, Wn.	Spring 1955
<i>T. Parryi</i>	Ownbey s.n. in 1948	8	36	Pullman, Wn.	Spring 1953
<i>T. Parryi</i>	Roeder 280	27	36	Pullman, Wn.	Spring 1955
<i>T. Rothrockii</i>	Beaman & Barclay 798	798	?	Native habitat	July 1954
<i>T. texensis</i>	Beaman 694	—	18	Native habitat	June 1954

¹ Original localities for this material may be found in the Systematic Treatment in the citations of specimens under the various species.

² Additional chromosome counts in *Townsendia* will be found in a previous paper (Beaman, 1954).

misidentified as *T. mensana*; *T. minima* (culture 3) = *T. montana* var. *minima*; *T. condensata* (culture 47) was misidentified as *T. spathulata*. The chromosome numbers of five species not included in the previous study are reported in Table I in the present paper.

Microsporogenesis in diploid, sexual plants

In all but one collection of the diploid material examined in this study, microsporogenesis was regular and nine bivalents were observed at metaphase I. In the exceptional collection (Beaman 945) at least one plant was characterized by 10 bivalents. Apparently the pairing attraction of the tenth chromosome pair was not very strong, as some cells were found with nine bivalents and two univalents instead of ten bivalents. Other material collected from this same population is characterized by nine bivalents at metaphase I and no meiotic irregularities. It seems probable that the ten-chromosome material is a rare abnormality.

An examination of the meiotic karyotype of *T. mexicana* revealed meiotic chromosomes of a smaller size than has been found in any other species of *Townsendia*. A metaphase plate from a preparation of *T. mexicana* is shown in Plate I, fig. 3. This figure may be compared with Plate I, fig. 2, which illustrates larger metaphase chromosomes typical in the genus. The karyotype of *T. annua*, the species morphologically most similar to *T. mexicana*, has not been examined.

Microsporogenesis in polyploid, apomictic plants

In the present study no special attempts have been made to obtain additional chromosome counts in apomictic material. Instead, investigations have been concentrated on material from apomictic populations of two species. These were chosen particularly because one is triploid and the other tetraploid. Both bivalents and univalents are found at metaphase I in the triploid. This stage in the tetraploid is characterized by 36 univalent chromosomes. The triploid material is from a population (culture 6) of *T. incana*. This species, especially this population, has been used extensively also in the investigation of megasporogenesis. Thus, comparative data of the male and female reproductive phases in the same population have been obtained. The tetraploid material is from a population (culture 8) of *T. Parryi*. Megasporogenesis in this population also has received attention.

Townsendia incana (culture 6). Meiosis in the anthers of plants of this population is characterized by a considerable

amount of chromosome pairings, as may be seen from Plate I, fig. 4. The number of bivalents in relation to the number of univalents is not constant. Mostly there are between five to ten bivalents and six to 15 univalents. No pollen mother cells with all univalents have been observed. Meiosis in the ovules, on the other hand, frequently is characterized by all univalent chromosomes at late prophase and metaphase (see Table III). Some variation of the chromosome number occurs within the population. In addition to the chromosome count of $2n = 28$ which was previously reported (Beaman, 1954), the count $2n = 27$ also has been obtained. From some of the examinations of microsporogenesis it appears that the number $2n = 26$ might occur in the population, but chromosome counts from microsporogenesis are difficult to obtain and often are unreliable. A variable chromosome number could be expected in the population, however, as a result of meiotic irregularities in megasporogenesis. Micronuclei, which have been observed with dyads of megaspores, probably represent chromosomes or chromosome fragments excluded during megasporogenesis. In this triploid population the loss or gain of a small amount of chromosomal material might not be lethal.

At anaphase I in culture 6, lagging univalents are frequently seen (Plate II, fig. 1). The halves of the bivalents go directly to the poles during anaphase I, but univalents seem to be much less strongly attracted to the poles. Usually the univalents eventually reach one of the poles, but sometimes they are excluded from the main nuclei and form micronuclei. Chromosome counts at metaphase II indicate that in the first division the triploid number of chromosomes is reduced by about half in the two resulting nuclei. Usually 12 to 15 chromosomes are seen at metaphase II. The distribution of the univalents at the first anaphase is unequal, and the two poles do not receive exactly the same number of chromosomes.

Tetrads of microspores in culture 6 (Plate II, fig. 2) have a fairly normal appearance. Their subsequent development, however, is not normal. Cell walls usually do not form between the microspore nuclei, and all four nuclei are surrounded by a wall which develops the structural characteristics of an ordinary pollen wall (Plate II, fig. 3). The ultimate "male gametophyte" which results from this type of development is a giant, several-nucleate pollen grain (Plate IV, fig. 2). At anthesis, in addition to the large grains, there are many aborted grains of various sizes. The determination, from herbarium specimens, of plants from apomictic populations is an easy matter when the pollen has been

formed in the manner outlined above. A reference to this peculiar method of pollen development was made by Holmgren (1919) in his study of *Erigeron*. He noted, in sexual material, that pollen of florets in a transitional position on the head between pistillate ray-florets and hermaphroditic disk-florets developed by wall formation around the four nuclei of the tetrad. He stated that this abnormality was not infrequently encountered in apomicts and hybrids. A few other references to this type of pollen development occur in the embryological literature.

Microsporogenesis and pollen development in culture 6 are of interest in regard to the recognition of apomixis in populations from herbarium specimens. However, since reduction occurs in this material, little information is gained on the mechanism of meiosis on the female side where reduction must be avoided. Tetraploid culture 8 of *T. Parryi* differs in its microsporogenesis from culture 6 of *T. incana* and possibly may have similar processes in both the male and female phases.

Townsendia Parryi (culture 8). Gustafsson (1934, 1935) has reviewed and defined three processes by which chromosome reduction may be avoided in apomicts during the development of the archesporial cell to form a female gametophyte. These processes have been termed "semiheterotypic division" (restitution nucleus formation), "pseudohomeotypic division" (a single division of the univalent chromosomes to form a dyad, not involving restitution nucleus formation), and "mitotic division" (the archesporial cell divides to form a dyad and no features of meiosis are found in the process). The process by which unreduced dyads are formed in *Townsendia* has some resemblance to a normal meiosis; thus, either the semiheterotypic or the pseudohomeotypic division must occur, and the mitotic type will not be further considered.

No anaphase restitution nuclei have been positively identified in *Townsendia* in mega- or microsporogenesis. It might seem, therefore, that the pseudohomeotypic division occurs in the genus. The univalent chromosomes observed in megasporogenesis in the apomicts might also be suggestive that the pseudohomeotypic division occurs in *Townsendia*. Especially, the occurrence, at diakinesis or prometaphase in megasporogenesis, of univalents with visible chromatids (Plate I, fig. 5) might indicate this type of division.

Fagerlind recently has examined megasporogenesis in apomictic material of *Rudbeckia* (1946), *Erigeron* (1947a), and *Taraxacum* (1947c), and microsporogenesis in apomictic *Hierac-*

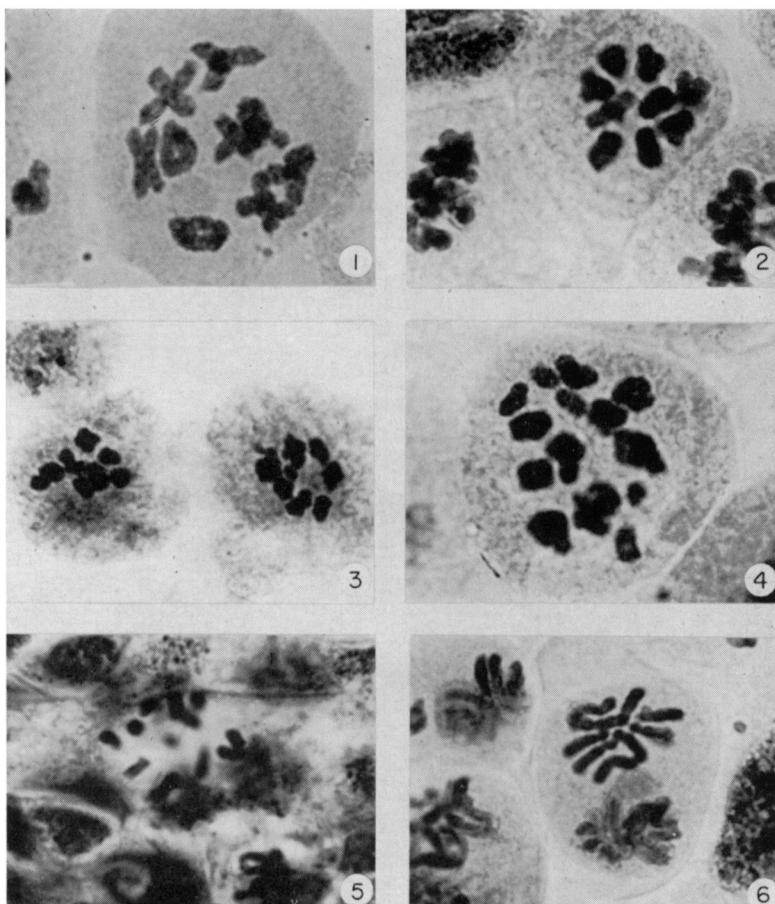


PLATE I. Photomicrographs of meiotic chromosomes in *Townsendia* (all $\times 1200$). Fig. 1. Nine bivalents at diakinesis in microsporogenesis in sexual, diploid *T. incana*. Fig. 2. Nine bivalents at metaphase I in microsporogenesis in *T. eximia*. Fig. 3. Nine bivalents at metaphase I in microsporogenesis in *T. mexicana*. The chromosomes are smaller in *T. mexicana* than those known in any other species of the genus. Fig. 4. Bivalent and univalent chromosomes at metaphase I in microsporogenesis in apomictic, triploid *T. incana*. Fig. 5. Univalent chromosomes at diakinesis or prometaphase in megasporogenesis in apomictic, triploid *T. incana*. The microtome blade bisected this cell, and the portion shown contains about half of the chromosomes. Fig. 6. Chromosomes at metaphase II in microsporogenesis in sexual, diploid *T. incana*.

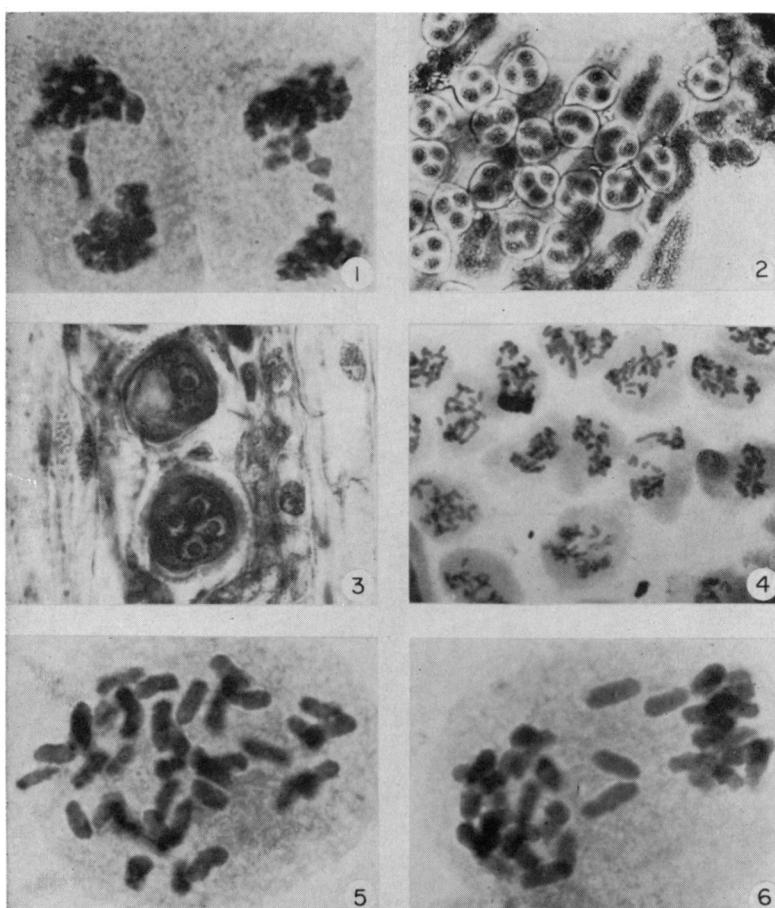


PLATE II. Some aspects of microsporogenesis in apomictic populations of *Townendia*. Fig. 1. Anaphase I with lagging univalent chromosomes in triploid *T. incana* ($\times 1200$). The halves of the bivalents go directly to the poles at anaphase I while the univalents lag. Usually the univalents reach one of the poles but sometimes they are incorporated into separate micronuclei. Fig. 2. Tetads in triploid *T. incana* ($\times 200$). These have the appearance of normal tetrads, but the microspores do not separate, and all four nuclei are incorporated within a single pollen grain. Fig. 3. Young pollen grains of triploid *T. incana* formed by the inclusion of a tetrad of microspores within one wall ($\times 470$). Fig. 4. Pollen mother cells with all univalent chromosomes in tetraploid *T. Parryi* ($\times 200$). Fig. 5. A more highly magnified view than fig. 4 of 36 univalent chromosomes at metaphase I in *T. Parryi* ($\times 1200$). Fig. 6. Anaphase I in tetraploid *T. Parryi* ($\times 1200$). This is an extreme anaphase. Usually these univalent chromosomes do not have a strong tendency to migrate to the two poles.

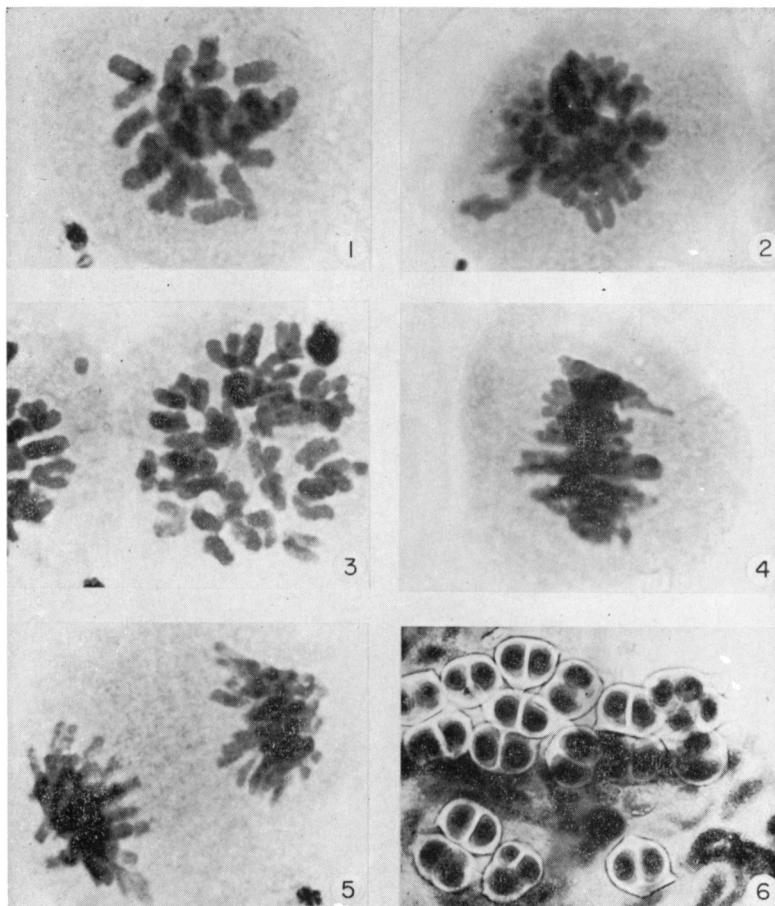


PLATE III. Some phases of microsporogenesis in apomictic populations of *Townsendia* (continued from Plate II). Fig. 1. A metaphase restitution or contraction nucleus composed of univalent chromosomes in tetraploid *T. Parryi* ($\times 1175$). Fig. 2. A restitution or contraction nucleus in tetraploid *T. Parryi* at a slightly later stage than that in fig. 1, showing chromatids of some of the chromosomes ($\times 1175$). Fig. 3. Polar view of metaphase II after the formation of the restitution or contraction nucleus in tetraploid *T. Parryi* ($\times 1175$). It is evident from this photograph that the chromosome number has remained unreduced. Reduction is prevented when all the chromosomes clump at metaphase I instead of migrating to the two poles and remaining there at anaphase I. Fig. 4. Side view of metaphase II in tetraploid *T. Parryi* ($\times 1175$). Fig. 5. Side view of anaphase II in tetraploid *T. Parryi* ($\times 1175$). Reduction did not occur at anaphase I and thus a dyad is formed at anaphase II. Fig. 6. Dyads in apomictic polyplloid *T. condensata* ($\times 200$). The two microspores develop separately into pollen grains. Apomicts which have all or nearly all univalent chromosomes at metaphase I form dyads rather than tetrads of microspores.

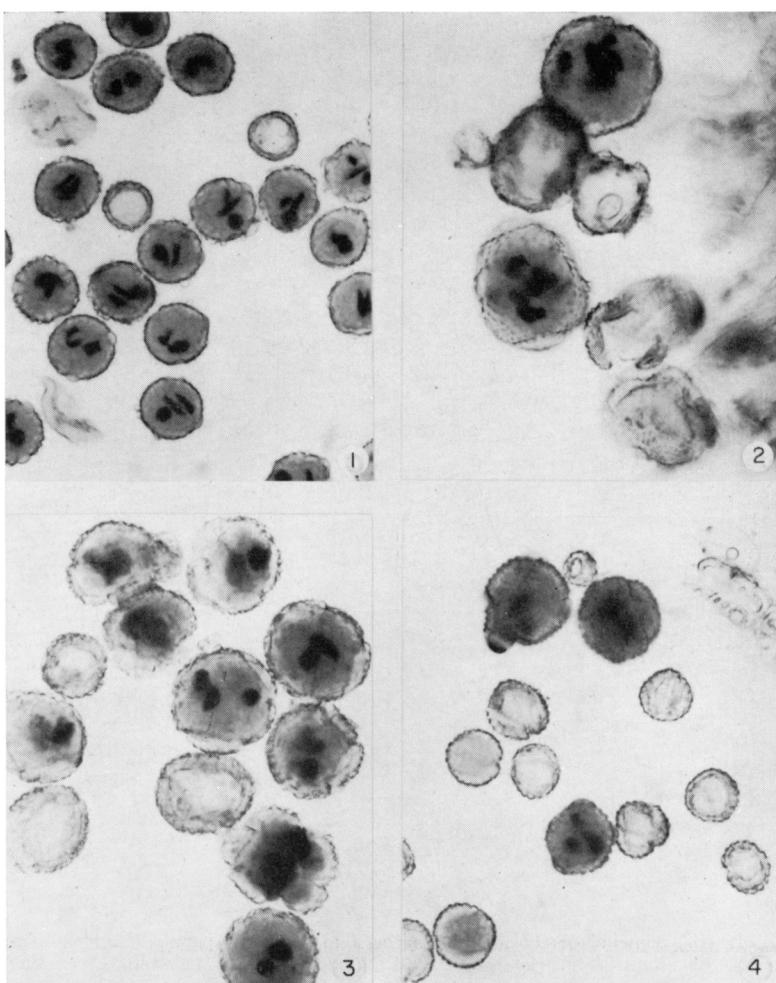


PLATE IV. Photomicrographs of pollen in sexual and apomictic populations of *Townsendia* (all $\times 330$). Fig. 1. Pollen of sexual, diploid *T. incana*. Fig. 2. Pollen of apomictic, triploid *T. incana*. These giant grains result from the incorporation of the four microspores of a tetrad into a single grain. Non-abortive grains contain more than three nuclei but these are so contorted that it is not possible to determine exactly how many are present. Fig. 3. Pollen of apomictic, tetraploid *T. Parryi*. These very large grains have developed from dyads similar to the ones shown in Plate III, fig. 6. The nuclei in these pollen grains have the unreduced, tetraploid chromosome number. Fig. 4. Pollen from a randomly selected herbarium specimen of *T. incana* (Walker 206). The percentage of aborted grains in apomicts is usually as high as or higher than that indicated here by the grains without nuclei.

ium (1947b). His observations in these genera have led him to doubt that the pseudohomeotypic division occurs frequently or that it even occurs at all. He emphasizes that restitution nuclei are not necessarily formed only at anaphase but may occur also at metaphase, prometaphase, diakinesis, or even earlier in prophase. Fagerlind especially stresses the fact that the "contraction nuclei" (a term coined by Rosenberg for the clumped meiotic chromosomes of *Hieracium*) he observed in *Erigeron*, *Hieracium*, *Taraxacum*, and *Rudbeckia* might be restitution nuclei which are formed at metaphase or earlier.

A clumping of meiotic chromosomes in several apomictic collections of *Townsendia* was reported in the previous cytogenetic study in this genus (Beaman, 1954). Clumped chromosomes in meiosis appear to be a regular feature in many apomictic forms. In *Townsendia*, the clumping in microsporogenesis is so prevalent in material from some populations that it defies analysis. In culture 8 of *T. Parryi*, however, it has been possible to analyze the various processes of the apomictic meiosis in microsporogenesis, and to determine the probable sequence of the meiotic stages. Smears have been used in this study in order to render visible as much as possible of the chromosomal detail. Fagerlind's studies apparently have all been made with sectioned material. Also, other investigators of the mechanism of the meiotic non-reduction phenomena have used mostly sectioned material. Sectioned microsporocytes of *Townsendia* are unsatisfactory for critical chromosomal analyses.

Bivalents have never been found in microsporogenesis in culture 8 of *T. Parryi*. When chromosomes become clearly evident in this material at diakinesis or prometaphase they are univalents. Whether the chromosomes were paired at an earlier stage and have come unpaired, or whether they were never paired, was not determined in this study. More refined cytological techniques will be required for the solution of that problem. Typical univalent chromosomes in this material are shown at two different magnifications in Plate II, figs. 4 and 5. Infrequently, a slight tendency is manifested for a migration of the univalents to the two poles (Plate II, fig. 6) at anaphase I. More frequently, a single clump of chromosomes is found at the center of the cell (Plate III, fig. 1). In some clumps, in cells which are apparently at slightly later stages (Plate III, fig. 2), the chromatids become evident. Seen in polar view at a still later stage, the clump is loosened and the chromatids are very conspicuous (Plate III, fig. 3). A count of the chromosomes at this stage indicates that

the number has not been reduced. After the anaphase that follows, the chromosomes in the resulting dyad have a telophase II or slightly mitotic aspect (Plate III, fig. 5). These are like telophase I chromosomes. A wall is formed after this division and an unreduced dyad results. Perhaps this dyad is homologous to those found after megasporogenesis! The "microspore dyads" which result after non-reductional meiosis soon separate into their component "microspores" and these may develop into normal-appearing (except for their large size) pollen grains (Plate IV, fig. 3). At anthesis many aborted grains of various smaller sizes are present also. It is therefore possible to detect these apomictic forms by herbarium specimens.

It appears, according to the events outlined above, that the univalents at metaphase I may undergo a migration toward the poles. The migration is weak, however, and two nuclei and a corresponding reduction in the chromosome number do not occur. Rather, the chromosomes are oriented into a single clump (contraction nucleus). While thus clumped, chromatid separation becomes evident. By the time the clump loosens, the chromatids are nearly separated. Anaphase II begins immediately and two unreduced nuclei result.

Discussion of microsporogenesis in polyploid, apomictic plants.

Fagerlind has stressed the point that at the time of formation of the contraction nucleus, a nuclear membrane re-encloses the chromosomal mass. No evidence of a nuclear membrane around the chromosome clumps has been detected in the smears of *Townsendia* microsporocytes. In sectioned preparations, the nuclear material is rather diffuse at this stage, but such figures might be interpreted as having a nuclear membrane around the chromosome clump. No indications of twisted or variously contorted chromosomal masses have been observed in smears of anthers of *Townsendia*. However, misshapen nuclei were seen at corresponding stages in sectioned material. It is possible that some of the details of Fagerlind's description of the metaphase restitution nucleus (contraction nucleus) are based on artifacts in his sectioned material. Smears are most useful for chromosomal analysis, and sectioned material is mainly valuable as a check for determining the proper sequences in meiotic development which are more difficult to determine in smears.

The evidence from smears of material of *Townsendia* seems to corroborate Fagerlind's idea of the significance of the clumped meiotic chromosomes. It seems probable that the genetic controls

of the rhythm of meiosis are such that, even in apomicts, univalent meiotic chromosomes cannot behave as ordinary mitotic chromosomes. Some of the features of the two-step meiotic cycle necessarily are retained. The tendency of univalents not to divide at first division is emphasized by univalent behavior in culture 6 of *T. incana*. In that material, the univalents regularly lag at anaphase I, and the chromatids do not separate until anaphase II. The chromosome clump at metaphase I in material with all univalents is actually equivalent to telophase I in normal, sexual material. In some of the apomicts meiosis may be impossible to analyze because the contraction nucleus or chromosome clump is formed earlier than metaphase. It appears, therefore, that the apomicts of *Townsендia* have a specialized type of meiosis (the semiheterotypic division) which avoids reduction of the chromosomes during microsporogenesis. From the present studies of megasporogenesis it seems probable that the type of meiosis outlined above for the male reproductive phase of culture 8 of *T. Parryi* may occur also in the female phase of this and the other apomictic populations of the genus.

It should be noted that Avers (1954) has produced evidence for the occurrence of a functional tertiary split of meiotic univalents in the microsporogenesis of triploid *Aster* hybrids. In her material univalent division appears to occur frequently at anaphase I in addition to the normal anaphase II division. No similar mechanism has been observed in *Townsендia*.

The peculiar alterations of microsporogenesis in the polyploid apomicts of *Townsендia* suggest a lack of functionality of the pollen which results. Also, it is unusual in these plants for the percentage of nucleated pollen to run higher than 20 per cent. Frequently this percentage is lower than five per cent, and sometimes no pollen is produced. Thus, the evidence from the male reproductive phase in the apomicts argues strongly for obligate apomixis in this genus. Evidence from the female reproductive phases reinforces this conclusion.

THE FEMALE REPRODUCTIVE PHASE

Investigations of the female reproductive phase in *Townsендia* have not been made previously. However, studies in other members of the *Compositae*, especially in *Erigeron*, are of significance to this study. Harling (1950, 1951a, and 1951b) recently has been making comparative embryological studies in certain tribes of the *Compositae*. His paper on embryology in the *Astereae* (1951b) includes investigations in 14 genera of this

tribe. Except for one genus, Harling found a single, constant type of embryo-sac development in the *Astereae*. This development is of the "normal," monosporic type with the production of an eight-nucleate embryo sac. The exceptional genus, *Erigeron*, has embryo-sac development of the normal type in some of its members, but also bisporic and tetrasporic developmental-types are found in the genus. Variation occurs both within and between species.

In the *Astereae* the only genus other than *Townsendia* now known to have apomictic forms is *Erigeron*. In the latter, asexual reproduction was known from embryo-sac studies as early as 1915 from a preliminary report by Tahara. Several investigators have made subsequent studies of apomixis in *Erigeron*. Fagerlind (1947a) has reviewed these investigations and given a new interpretation regarding the mechanism of non-reduction in the meiosis of apomicts of *Erigeron*. His ideas have been considered in detail in this paper under the section on microsporogenesis in apomictic plants.

The features of both sexual and apomictic reproduction in *Townsendia* are very similar to those in *Erigeron*. The processes in apomictic reproduction in these two genera are not known to be exactly duplicated in any other genus. Thus, the results of the investigations in *Erigeron* have significance in the interpretation of the embryological phenomena in *Townsendia*.

The female reproductive phase in sexual plants

Material of *Townsendia incana* has been more extensively used than that of any other species in the investigation of sexual and apomictic reproduction in the genus. Several populations of both sexual and apomictic types have been available for study. Comparisons of the two types of reproduction are therefore possible within a single species. Sufficient material of other species also has been available to indicate that most of the reproductive phenomena encountered in *T. incana* occur in other members of the genus.

Townsendia incana (culture 971). This species, as is characteristic for the genus, has a single archesporial cell in each ovule. The early prophase stages of meiosis are morphologically similar in all the material thus far examined, including the apomicts. It does not seem possible with the present techniques to determine at early prophase whether the chromonematal strands are unpaired, pairing, or paired. Therefore, the terms leptotene, zygotene, and pachytene are not used. A frequently encountered fea-

ture at early prophase is the so-called synezis which consists of clumped chromonematal material and an associated, distinct nucleolus. Synezis generally is considered to be an artifact present at zygotene and pachytene. It occurs in the prophase stages of both sexual and apomictic types of *Townsendia* (Plate V, figs. 3 and 4). Diakinesis is characterized by bivalents with pairing configurations similar to diakinesis division-figures in microsporogenesis (cf. Plate I, fig. 1 and Beaman, 1954, p. 173). No metaphase stages were encountered in culture 971.

In the one dyad observed in culture 971 no cell plate was present. At the tetrad stage and at subsequent stages certain peculiarities become evident. Twenty-one ovules were observed in which no nuclei of the tetrad were separated by cell walls. These, with the exception of one tetrad which still possessed a phragmoplast between two of the nuclei and was thus too young for determination, may be considered as 4-nucleate coenomegasporangia. The megasporangium nuclei are arranged in a linear fashion, and, usually, the nucleus nearest the micropyle is separated by a considerable distance from the other three nuclei. Ten tetrads were observed which had cell walls between the micropylar and submicropylar megasporangium nuclei (the micropylar megasporangium nucleus is the one nearest the micropylar end of the ovule, etc.). Eight tetrads were found with a wall between the submicropylar and subchalazal megasporangium nuclei. In one ovule the cell wall had formed on the micropylar side of the micropylar megasporangium nucleus.

In Harling's (1951b) study of *Erigeron*, he noted variations in wall formation in tetrads. Some of his material was characterized by no walls; some had wall formation apparently after metaphase I, some apparently after metaphase II, and some by wall formation after both meiotic divisions. He inferred the time of wall formation from the position of the walls relative to the nuclei of the tetrad. In *Erigeron glabellus* he found all of these conditions in a single plant. In *Townsendia incana* the occurrence of a wall outside of the tetrad, separating none of its nuclei, suggests that wall formation between the nuclei of tetrads has no perfect synchronization with the meiotic divisions. Furthermore, in much of the sexual *Townsendia* material, the abundance of walls between only the micropylar and submicropylar megasporangium nuclei, without corresponding walls between the chalazal and subchalazal megasporangium nuclei, suggests some lack of correlation of wall formation with meiotic division.

In culture 971, tetrasporic embryo sac development is most

common, but also one of the megasporic nuclei may degenerate and the other three germinate to form a three-nucleate embryo sac. This fact is indicated by the observation of two three-nucleate and two six-nucleate embryo sacs. However, tetrasporic development must be more frequent than other types in this population (cf. Table II). The embryo sac becomes morphologically organized after two series of mitotic divisions.

Sufficient observations in culture 971 have not yet been made to permit a full understanding of the great amount of variability in nuclear number in embryo sacs above the eight-nucleate level. This type of variability has been observed also in several other composite genera, particularly in *Erigeron* (cf. Harling, 1951b). In regard to several species of *Erigeron*, Harling states that in the development of the female gametophyte, one or more of the chalazal nuclei "strike" (i.e., cease dividing while others continue). Nuclear fusions in the embryo sacs of some plants, including *Erigeron*, have been noted. However, nothing which might indicate nuclear fusion has been observed in any of the material of *Townsendia*. Thus, it seems plausible that the variable number of nuclei in the embryo sac in culture 971 results from the "strike" of some of the chalazal nuclei at either or both of the postmeiotic divisions.

A statement is necessary in regard to the rather large amount of aborted and undetermined ovules of culture 971 (recorded in Table II). Some of this material was fixed after two or three nights with frosts, and it appears probable that freezing had adverse affects. Material from the same plant fixed before the frosts was not affected.

Townsendia incana (cultures 5 and 802). No material at a stage later than the beginning of female gametophyte development has been available from these populations. Fewer meiotic stages, also, were examined in these ovules than in those of culture 971, but no significant differences in meiosis in the three populations were noted. A difference is apparent at the tetrad stage, however. In cultures 5 and 802 a wall and a space regularly separate the micropylar nucleus from the other three members of the tetrad (Plate VI, fig. 4). A sufficient number of later stages has not been seen to permit conclusions regarding further development of the embryo sac in these two populations, but the female gametophyte is initially three-nucleate from the development of the three chalazal megasporic nuclei and the abortion of the micropylar nucleus.

A difference in genetic constitution probably is responsible

TABLE II.

Comparative classification of ovule development in five sexually reproducing populations of three species of *Townsendia*.¹

Developmental stage in ovule	Numbers of ovules observed in the populations (cultures)					
	971	5	802	35-I ²	35-II	39
Archesporial cell	2	—	1	1	—	—
Early prophase	6	3	4	10	—	2
Diakinesis	2	—	3	7	—	1
Diakinesis ?	—	—	1	—	—	—
Metaphase I	—	3	2	—	—	—
Anaphase I	—	—	1	—	—	—
Dyad	1	2	2	6	—	1
Metaphase II	1	1	—	—	—	1
Tetrad	43	86	44	31	—	20
Tetrad ?	—	2	—	—	—	—
2-nucleate embryo sac	—	—	—	—	—	3
3-nucleate " " ?	2	4	17	6	—	48
3-nucleate " "	—	1	1	1	—	3
4-nucleate " " ?	18	—	—	92	—	—
4-nucleate " "	1	—	—	2	—	—
5-nucleate " "	—	—	—	—	—	2
6-nucleate " "	2	—	—	2	—	17
6-nucleate " " ?	—	—	—	1	—	—
7-nucleate " "	—	—	—	1	—	—
8-nucleate " "	5	—	—	18	—	1
8-nucleate " " ?	—	—	—	1	—	—
9-nucleate " "	2	—	—	—	—	—
10-nucleate " "	—	—	—	3	—	—
11-nucleate " "	1	—	—	2	—	—
12-nucleate " "	3	—	—	31	—	5
12-nucleate " " ?	—	—	—	1	—	—
13-nucleate " "	1	—	—	—	—	—
14-nucleate " "	—	—	—	3	—	—
14-nucleate " " ?	—	—	—	1	—	—
15-nucleate " "	1	—	—	5	—	—
16-nucleate " "	—	—	—	7	—	—
16-nucleate " " ?	—	—	—	1	—	—
Egg and unfused polars	1	—	—	67	3	4
Egg and unfused polars ?	—	—	—	1	—	—
Egg and fusing polars	—	—	—	19	11	3
Egg and fusing polars ?	—	—	—	—	4	—
Egg and fused polars	—	—	—	—	1	—
Egg and fused polars ?	—	—	—	—	6	—
Embryo and endosperm	—	—	—	—	32	—
Not fertilized (disintegrating)	—	—	—	—	20	—
Abortive	17	—	—	13	5	2
Not determined	14	7	5	11	8	10
Total	123	109	81	344	90	123

¹ *Townsendia incana* (cultures 971, 5, and 802), *T. montana* var. *montana* (culture 35), and *T. grandiflora* (culture 39).

² Explanation of the culture-series symbols will be found in the text, pp. 28-33.

for the differences in tetrad-wall formation between culture 971 and the other two populations of *T. incana*. However, since the plants were grown in a different environment, and the buds were fixed at different seasons, environmental factors cannot be entirely disregarded as a possible influence. Positive conclusions about this type of variation will require further study.

Townsendia grandiflora (culture 39). One collection of this species was studied. The meiotic prophase is similar in all details to that described for culture 971 of *T. incana*. The tetrads, like those of cultures 5 and 802 of *T. incana*, are characterized by having a wall regularly formed between the micropylar and sub-micropylar megasporangium nuclei. The micropylar megasporangium nucleus also is separated by a considerable distance from the other three nuclei.

The series of developmental stages examined in *T. grandiflora* is complete enough to indicate that embryo sac development in this population is usually trisporic. Harling designated some of his *Erigeron* material as pseudotrisporic when, from the four-nucleate coenomegasporangium, only three of the tetrad nuclei gave rise to the embryo sac and the other nucleus degenerated. In addition to *Erigeron*, this condition has been recorded also by Harling in *Chrysanthemum* (1951a), *Anthemis* (1950), and *Matricaria* (1951a) and by Fagerlind (1941) in *Chrysanthemum*. Mauritzon (1933) has reported for the crassulaceous species *Aldasorea* (*Aeonium*) *guttata* (*nom. nud.*P) that sometimes a single megasporangium nucleus was separated from the other three of the tetrad by a wall. Subsequent embryo sac development could therefore be monosporic or trisporic, and Mauritzon has illustrated a 12-nucleate embryo sac (p. 28, fig. 9G) presumably of trisporic origin. Unfortunately his culture was lost before adequate developmental stages were obtained and before voucher specimens were prepared; thus, some doubt is left as to the identity of this material. In *Townsendia grandiflora* and in other populations of this genus which have a wall separating one nucleus of the tetrad from the other three, embryo sac development is trisporic. Thus, *Townsendia* may well be the first genus in which true trisporic embryo sac development is adequately documented.

In culture 39 of *T. grandiflora*, trisporic development is most frequent, but bisporic or pseudobisporic development may occur infrequently. Occasional two-nucleate embryo sacs have been observed. It seems probable that the initial development was

trisporic; then one of the three nuclei of the female gametophyte disintegrated at about the time the other two began enlarging previous to their first mitotic division. The nucleus nearest the chalazal end of the embryo sac frequently is weak (Plate IX, fig. 1). Thus, these two-nucleate embryo sacs probably are the result of pseudobisporic development because no tetrads were observed which exhibited wall formation anywhere but between the micropylar and submicropylar megasporangium nuclei.

The occurrence of five-nucleate embryo sacs in *T. grandiflora* seems to be the result of a "strike" by the chalazal-most nucleus at the first post-meiotic division. An eight-nucleate embryo sac observed in this material had already reached the morphological organization stage; presumably it was produced by pseudo-bisporic development and two subsequent series of mitotic divisions.

The antipodal cells observed in *T. grandiflora* were one-nucleate. Disintegration of these begins soon after morphological organization of the 12-nucleate embryo sac. When disintegration has commenced, it becomes very difficult to determine the total nuclear number of the female gametophyte. Later stages are designated according to the position of the polar nuclei. (The "unfused polars" stage is earlier than the "fusing polars" stage.)

Townsendia montana var. *montana* (culture 35). A considerable range of developmental stages in this population has been available in the present study. The stages of prophase differ in no visible manner from those described under *T. incana* (culture 971). The cell plate, an uncommonly seen feature in megasporogenesis, was observed in one dyad (Plate VII, fig. 1). This is the only instance in the examination of sexual material that a cell plate has been found in a dyad. Apparently this structure has a very short duration, and no wall formation follows its occurrence.

Tetrads with no walls between the nuclei (four-nucleate coenomegasporangia) and tetrads with a cell wall between the micropylar and submicropylar megasporangium nuclei were encountered in about equal numbers in this material. The micropylar nucleus is always separated by a considerable distance from the other three nuclei, whether or not a wall is present in this position. Since a larger number of four-nucleate than three-nucleate embryo sacs was found, it seems probable that all four megasporangium nuclei may sometimes germinate to form the four-nucleate female gametophyte, even though a wall separates one nucleus from the

other three. A few cases were observed in which this wall between the micropylar and submicropylar nuclei appeared to be disintegrating.

Eight-nucleate embryo sacs observed in the preparations of *T. montana* are the result of one post-meiotic division of the four megasporic nuclei and are not ready for morphological organization until another mitotic division occurs. The preponderance of 12-nucleate embryo sacs over those with 16 nuclei may indicate trisporic development or may result from a "strike" of the four nuclei at the chalazal end of the embryo sac at the second post-meiotic division. The 14- and 15-nucleate embryo sacs indicate a strike of one or two of these chalazal nuclei. The occurrence of 10- and 11-nucleate embryo sacs might be the result of the disintegration of some of the nuclei at the chalazal end of the embryo sac between the time of the first and second post-meiotic divisions.

In this population of *T. montana* the antipodal cells are better developed than in any other material of *Townsendia* yet examined. Ordinarily in *T. montana* there are three large antipodal cells (Plate XI, fig. 1) and four small ones at the extreme chalazal end of the embryo sac. All the antipodal cells are uninucleate.

Since conditions at or after anthesis in sexual material are important as a standard of comparison with the apomictic forms of *Townsendia* at corresponding developmental stages, a number of ovules of *T. montana* at these stages were examined. It should be noted that no stages later than embryo sacs with eggs and fusing polar nuclei have been found in pre-anthesis material from any of the sexual forms.

In material collected at and past anthesis only three instances of developmental stages earlier than the stage with polar nuclei beginning to fuse were encountered. One sure example of fused polar nuclei was found and six probable cases were noted. Apparently fusion is completed at about the time of fertilization since one embryo sac was observed in which the egg was still undivided but the primary endosperm nucleus was at telophase. In ovules from florets slightly past anthesis either an embryo and endosperm are present, or the interior of the ovule is in the process of disintegration. The latter condition probably results if fertilization does not occur.

The female reproductive phase in apomictic plants

Most of the investigation of apomixis in *Townsendia* has been concentrated on *T. incana*. Culture 6 of this species, which has

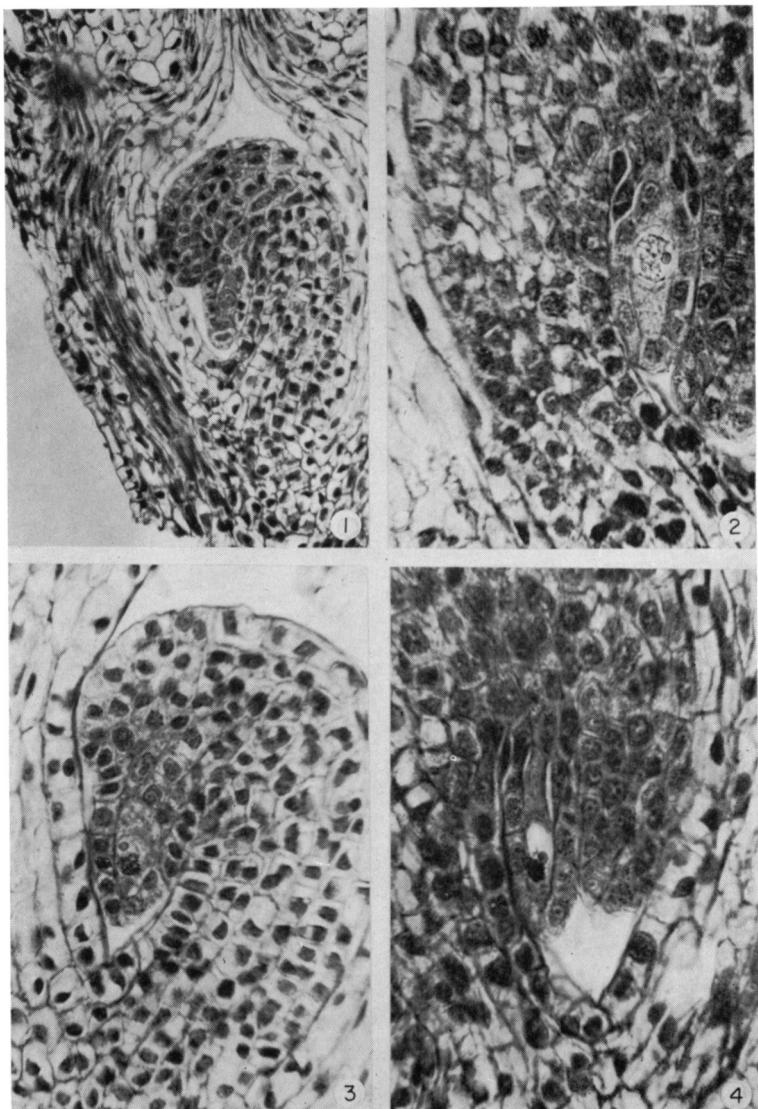


PLATE V. Photomicrographs of longitudinal sections of young ovules in *Townsendia*. Fig. 1. An incompletely inverted ovule of apomictic, triploid *T. incana* ($\times 220$). The nucellar epidermis surrounding the single archesporial cell has not been completely inclosed by overgrowth of the integument. Fig. 2. Early prophase of meiosis in apomictic, triploid *T. incana* ($\times 400$). This part of meiosis in the apomicts differs in no visible way from the corresponding stage in sexual plants. It is not possible to determine in this preparation whether or not the chromatin threads are paired. Fig. 3. Early prophase of meiosis in sexual diploid *T. incana* ($\times 400$). Synezesis apparently results during fixation at this stage. Fig. 4. Early prophase of meiosis in apomictic, triploid *T. incana* ($\times 400$). Synezesis is a prophase feature in both sexual and apomictic material.

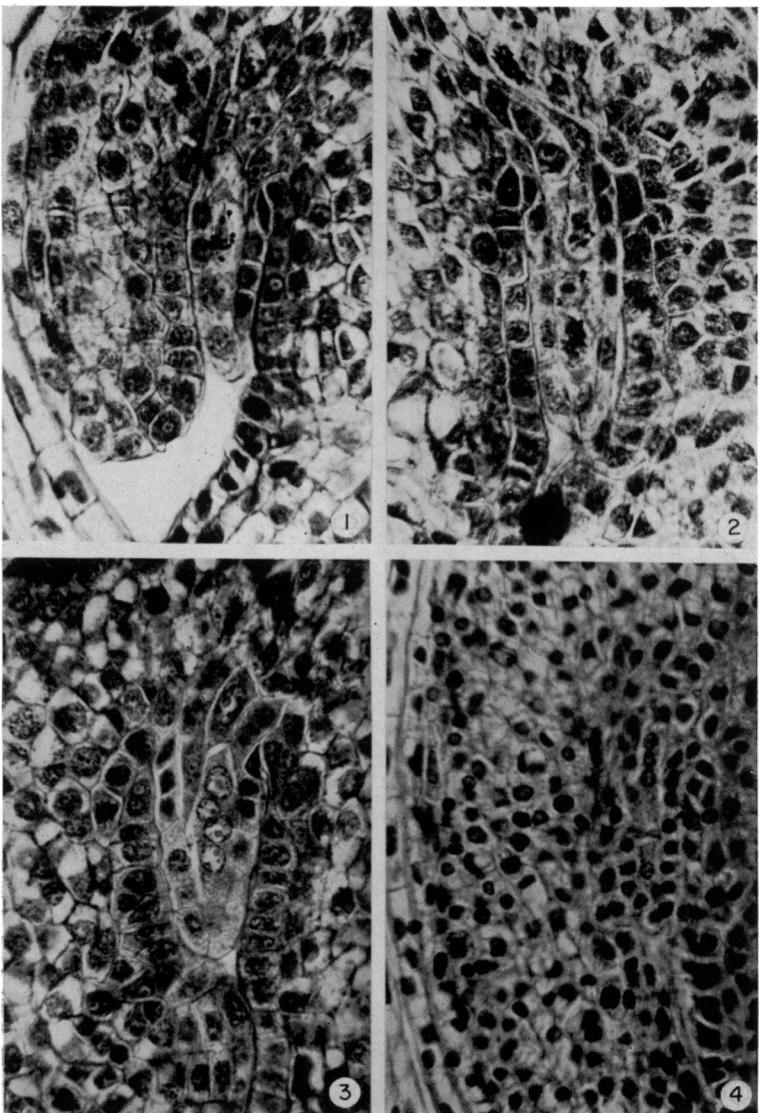


PLATE VI. Photomicrographs of longitudinal sections of ovules in *Townsендия* (all $\times 400$). Fig. 1. Metaphase I with clumped and scattered univalents in apomictic, triploid *T. incana*. Fig. 2. Anaphase II in apomictic, triploid *T. incana* with three extra groups of chromosomes excluded from the two main nuclei at anaphase I. Fig. 3. A tetrad of megasporangium nuclei (4-nucleate coenomegasporangium) in apomictic, triploid *T. incana*. Fig. 4. A tetrad of megasporangium nuclei with the nucleus at the micropylar end of the tetrad separated by a space and a wall from the other three megasporangium nuclei, in sexual, diploid *T. incana*. Embryo sac development is trisporic from tetrads of this type.

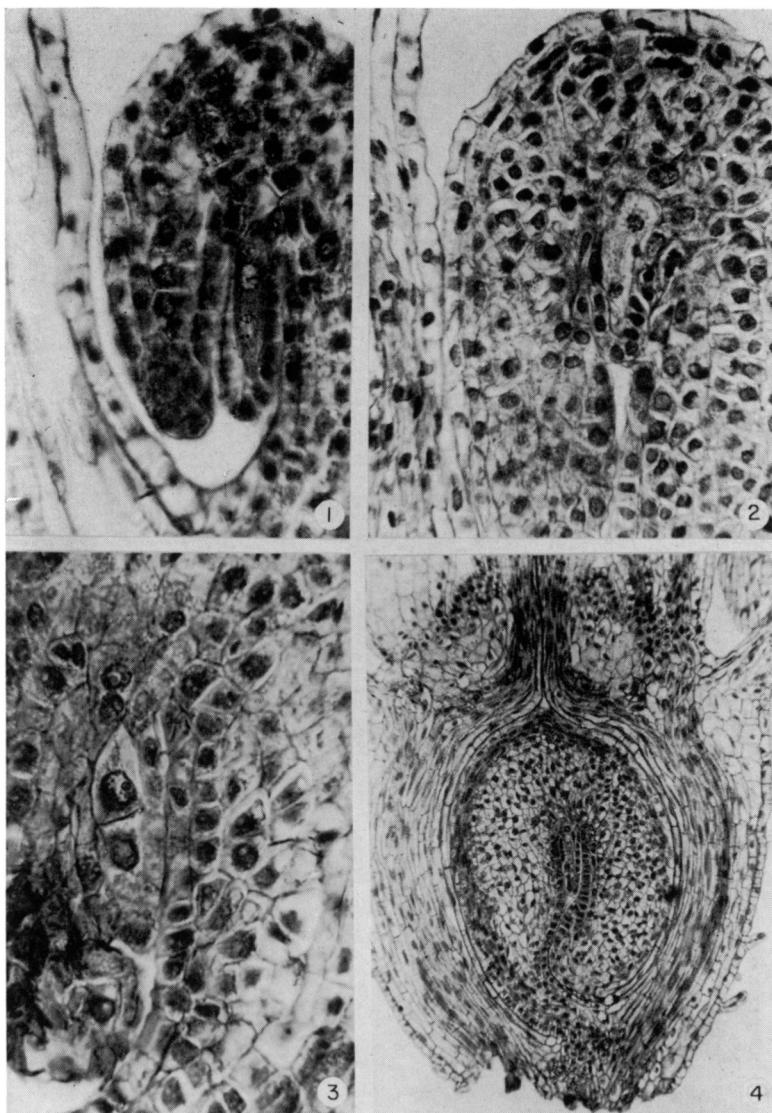


PLATE VII. Photomicrographs of longitudinal sections of ovules and ovaries in *Townsendia*. Fig. 1. Dyad of sexual, diploid *T. montana* var. *montana*, showing a cell plate ($\times 400$). Fig. 2. Dyad of sexual, diploid *T. incana*, without cell plate ($\times 400$). This is the most frequently encountered type of dyad in sexual material. Fig. 3. Dyad of apomictic, polyploid *T. Rothrockii* ($\times 400$). This is the only population of *Townsendia* known to have walls separating the dyad nuclei. Fig. 4. Ovule and ovary at the dyad stage in apomictic, triploid *T. incana* ($\times 185$).

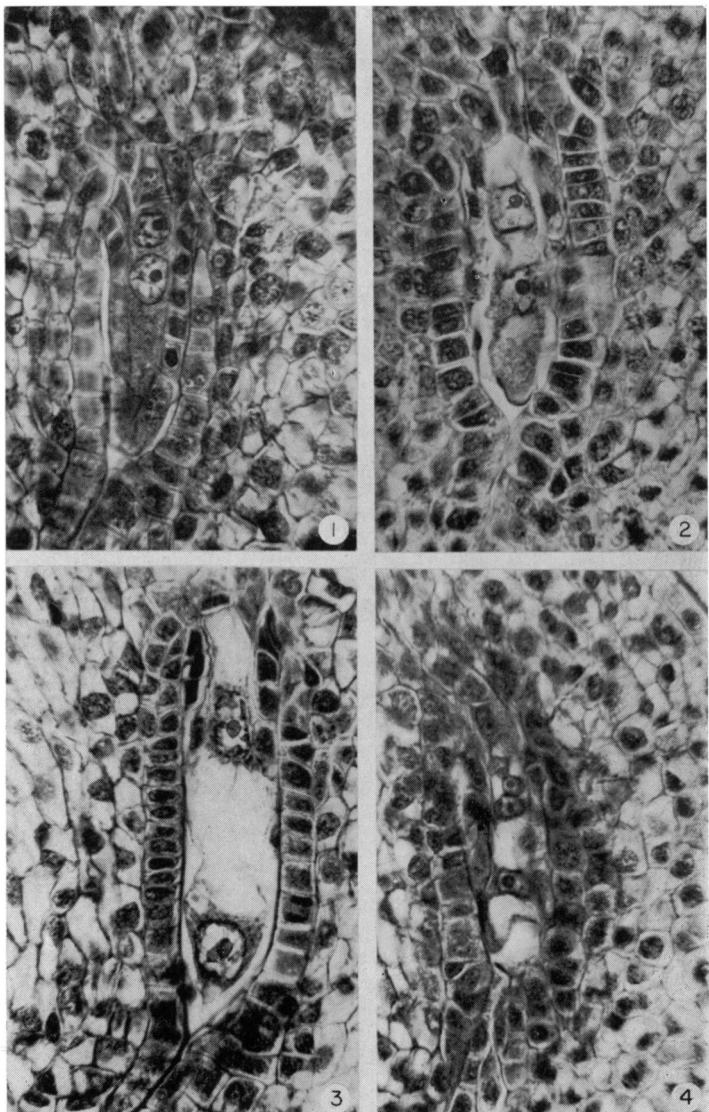


PLATE VIII. Photomicrographs of longitudinal sections of ovules in apomictic, triploid *T. incana* (all $\times 400$). Fig. 1. Dyad. Fig. 2. A very young 2-nucleate embryo sac which has developed from an unreduced dyad. At the time of fixation the nucellar epidermis was in the process of disintegration and the embryo sac was expanding, filling the cavity formed by the overgrowth of the integument. Fig. 3. A 2-nucleate embryo sac with the nuclei at prophase. Fig. 4. A young 4-nucleate embryo sac. This embryo sac is the result of tetrasporic development of a 4-nucleate coenomegaspore.

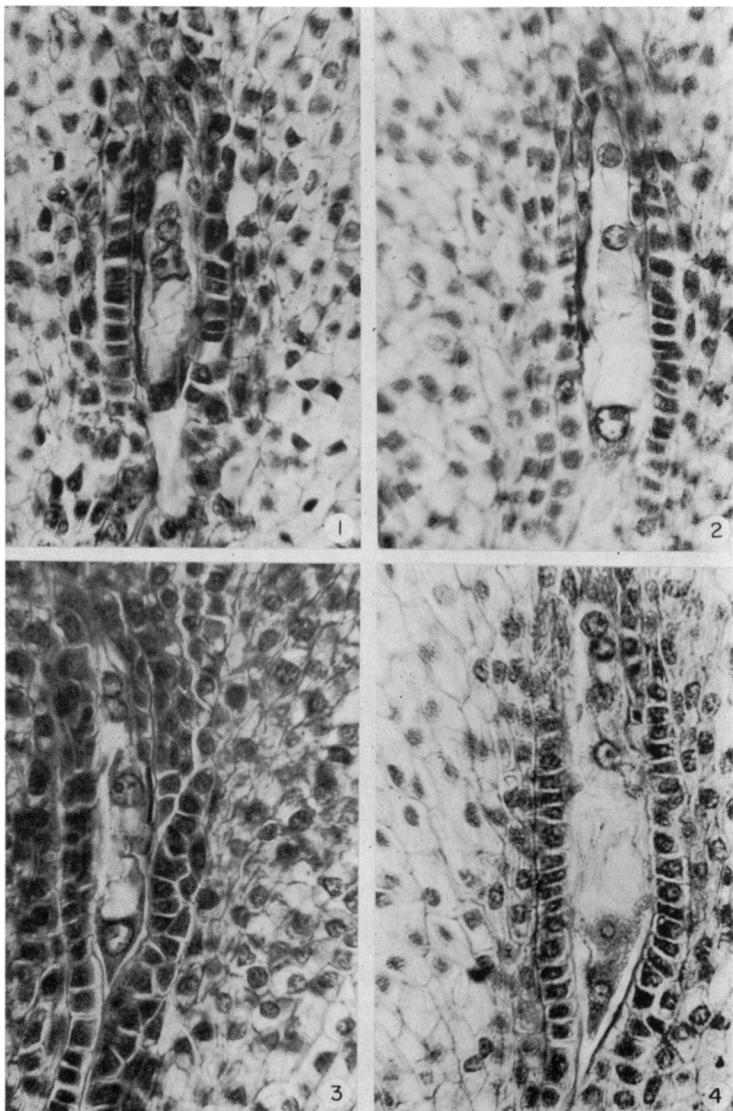


PLATE IX. Photomicrographs of longitudinal sections of ovules in *Townsendia* (all $\times 400$). Fig. 1. A very young 3-nucleate embryo sac, the result of trisporic development, in sexual, diploid *T. grandiflora*. At the time of fixation the nucellar epidermis was in the process of disintegration. The remnants of the fourth megasporangium nucleus and part of the nucellar epidermis are evident at the micropylar end of this embryo sac. Fig. 2. A 3-nucleate embryo sac which has resulted from trisporic development in sexual, diploid *T. grandiflora*. Fig. 3. A 4-nucleate embryo sac which has resulted from tetrasporic development in sexual, diploid *T. montana*. Fig. 4. A 6-nucleate embryo sac in sexual, diploid *T. grandiflora*. The six nuclei are the result of one mitotic division-series in a 3-nucleate embryo sac of the type shown in fig. 2.

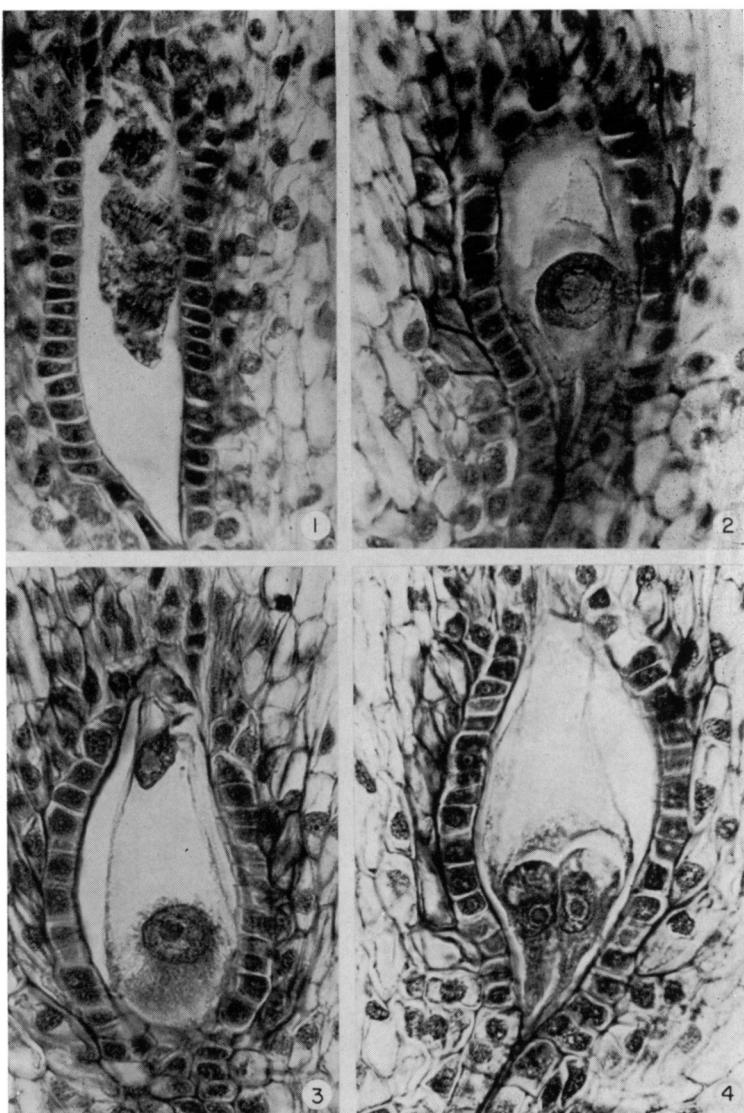


PLATE X. Photomicrographs of longitudinal sections of embryo sacs in apomictic, triploid *T. incana* (all $\times 400$). Fig. 1. A 4-nucleate embryo sac with all four nuclei at metaphase. Figs. 2-4. The egg cell (fig. 2), the unfused polars (fig. 3), and the synergids (fig. 4) in serial sections through a single embryo sac. At this stage the antipodals have already disintegrated.

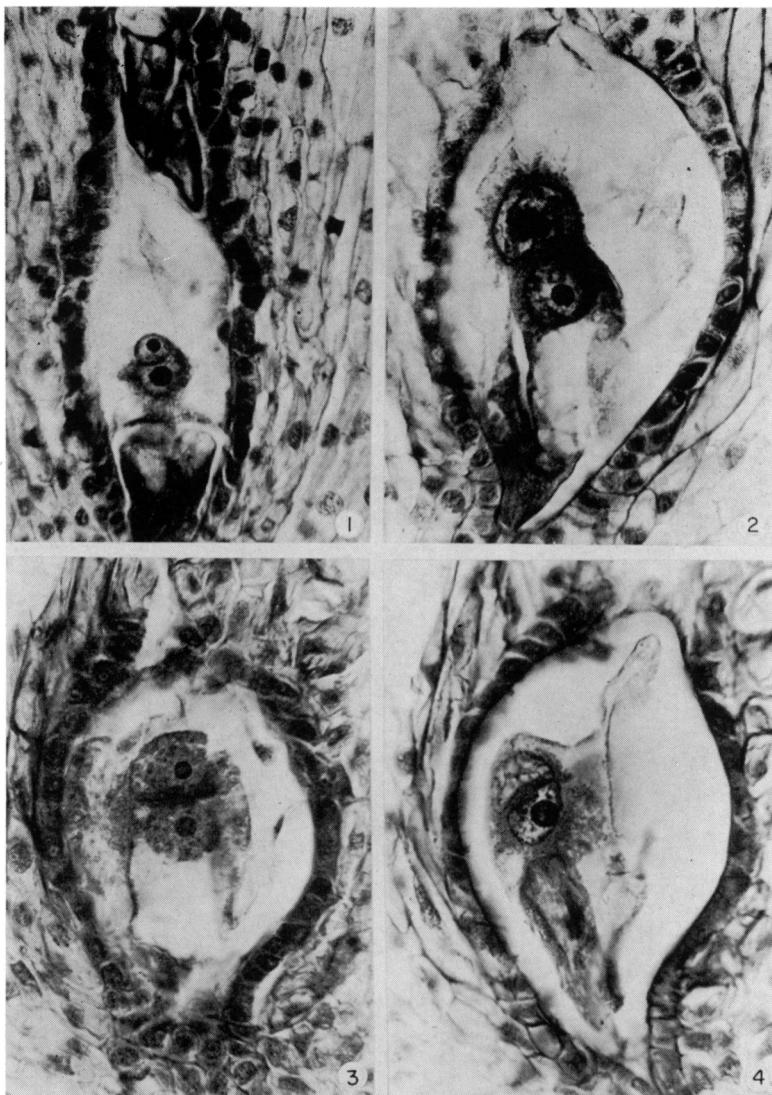


PLATE XI. Photomicrographs of longitudinal sections of embryo sacs in *Townsendia* (all $\times 400$). Fig. 1. A 12-nucleate embryo sac in sexual, diploid *T. montana* var. *montana*. Three large antipodal cells are shown in the upper portion of this figure; four smaller antipodal cells farther toward the chalazal end were excluded in this figure. *Townsendia montana* is the only species of the genus presently known to have well-developed antipodal cells. The egg cell was included in an adjacent section. The two conical-shaped synergid cells are immediately below the fusing polar nuclei in this figure. Fig. 2. The egg and fusing polar nuclei in apomictic, triploid *T. incana*. Portions of the synergids are at the bottom of the figure. Figs. 3-4. Adjacent sections of an embryo sac in apomictic, triploid *T. incana*. The 2-nucleate proembryo (fig. 3) is associated with fusing polar nuclei (fig. 4).

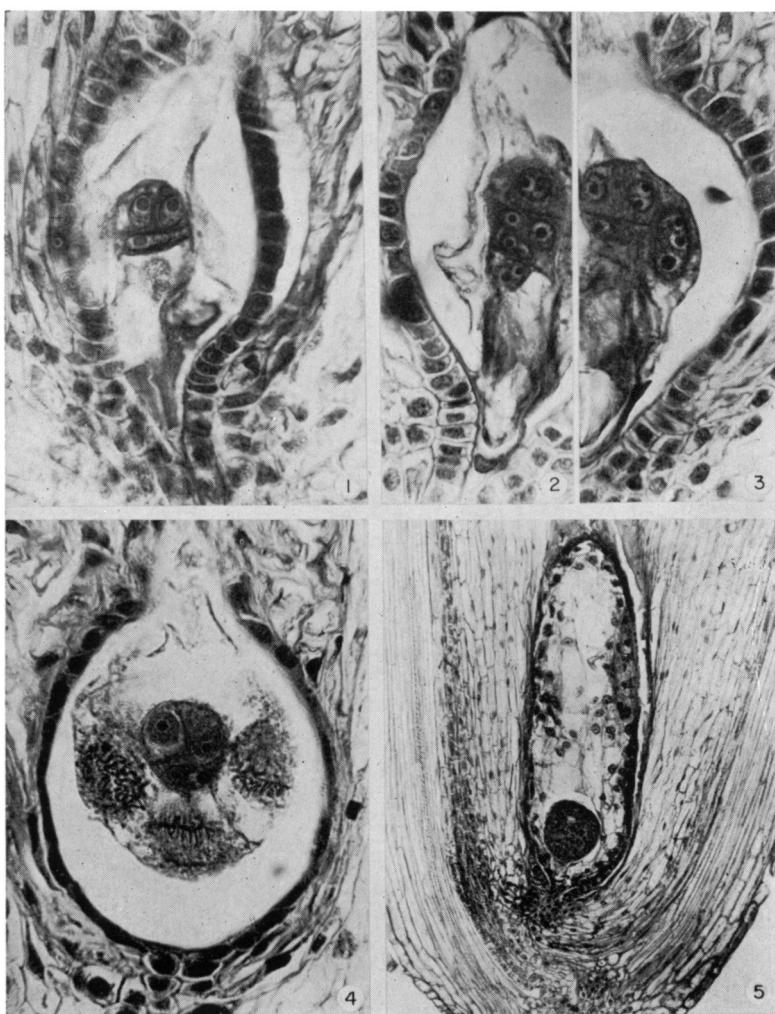


PLATE XII. Photomicrographs of longitudinal sections of embryo sacs, with embryos, in apomictic, triploid *Townsendsia incana*. Figs. 1-4 from florets at pre-anthesis stages. Fig. 1. A 4-celled embryo ($\times 350$) accompanied (in another section) by fusing polar nuclei similar to those shown in Plate XI, fig. 4. One of the intact, conical-shaped synergid cells is at the lower right of the embryo. Figs. 2-3. Adjacent sections in an embryo sac showing an 8-nucleate proembryo, accompanied by 4-nucleate endosperm (three of the endosperm nuclei were not included in this section) ($\times 350$). At the time of fixation, the three apical nuclei of this embryo had not been separated by walls. Fig. 4. A non-median section showing 3 of the 8 endosperm nuclei in this embryo sac at metaphase ($\times 350$). Fig. 5. A portion of the ovary and its contents from a floret just past anthesis ($\times 90$).

been used most extensively, was grouped into five series according to the stages selected for examination and the conditions under which it was grown. Series I-IV were grown in Cambridge, Massachusetts and fixed in November, 1955. Series V was grown in Pullman, Washington and fixed in the spring of 1955.

Townsendia incana (culture 6-I). The material of this series was taken from five plants. The developmental stages of the florets ranged from pre-meiotic to pre-anthesis. Early prophase of megasporogenesis is similar in appearance in sexual and apomictic forms (Plate V, figs. 2 and 4). Synezesis is as frequent in the early prophase stages in the apomicts as in the sexual material. Diakinesis is the earliest stage at which differences between the sexual and the apomictic types become apparent. At this stage both megaspore mother cells with all the chromosomes unpaired and those with some pairing have been observed. In sectioned material it is often difficult to determine how many chromosomes are present and whether or not they are paired. Accurate appraisals are possible only in very good preparations.

Metaphase configurations with all univalent chromosomes and those with some of the chromosomes paired have been found in this apomictic form. A metaphase figure with univalents scattered along the spindle is shown in Plate 6, fig. 1. Fagerlind (1946, 1947a, 1947b, 1947c), in his publications on the mechanism of apomictic megasporogenesis, has considered the scattered-univalent configuration to be a stage just preceding formation of the metaphase restitution nucleus. Interpretation of this feature in megasporogenesis in *Townsendia* is not attempted at this time. Smears of anthers at the proper stages are more amenable to interpretation of the mechanism of the apomictic meiosis, and the problem is more fully considered under the section in this paper on the male reproductive phase.

Megaspore tetrads are rare in this apomictic population of *T. incana* (cf. Table IV). The most normal-appearing tetrad which has yet been found is shown in Plate VI, fig. 3. It should be noted that no walls separate the megaspore nuclei. When reduction occurs, embryo sac development is tetrasporic (Plate VIII, fig. 4). Tetrads indicate reduction in the chromosome number. This fact is evident from the study of microsporogenesis in *Townsendia*. In this triploid, apomictic material, nuclei with a reduced chromosome number probably cannot function in the production of new embryos. It appears improbable that the few eggs which might develop with the reduced chromosome number would be fertilized by functional sperms, especially since the

TABLE III.

Comparative classification of ovule development in six apomictically reproducing populations of three species of *Townsendia*.¹

Developmental stage in ovule	Numbers of ovules observed in the populations (cultures)							
	6-Ia ²	6-II	6-Va	17-I	875	8	27	798
Archesporial cell	—	11	—	—	2	2	—	6
Early prophase	14	53	10	28	5	5	2	22
Diakinesis (all univalents)	1	—	—	1	—	—	—	—
Diakinesis (some pairing)	—	1	—	—	—	—	—	—
Diakinesis (pairing not det.) ...	—	3	6	9	4	1	3	3
Prometaphase (all univalents) ...	2	—	—	—	1	—	—	—
Metaphase I (all univalents) ...	1	1	—	—	—	2	—	—
Metaphase I (some pairing)	2	1	—	—	—	—	—	—
Metaphase I (pairing not det.)	—	1	3	4	—	1	2	1
Anaphase I	—	—	1	5	1	—	—	—
Dyad	96	47	23	69	32	64	8	9
Dyad with micronuclei	5	1	2	—	—	—	—	—
Dyad ?	3	—	—	—	—	—	—	—
Metaphase II	1	—	—	—	—	—	—	—
Anaphase II	1	1	—	—	—	—	—	—
Tetrad	4	5	—	2	—	4	—	11
Tetrad with micronuclei	2	—	—	1	—	—	—	—
Double tetrad	1	—	—	—	—	1	—	—
Tetrad ?	2	1	—	—	—	—	—	—
1-nucleate embryo sac	6	—	—	—	—	—	—	—
1-nucleate " " ?	12	—	—	—	—	—	—	—
2-nucleate " "	110	30	7	12	55	1	14	—
2-nucleate " "	—	—	—	1	—	—	—	—
(with micronuclei)								
2-nucleate embryo sac ?	19	3	—	—	—	—	—	—
3-nucleate " "	1	—	—	—	1	—	—	—
4-nucleate " "	38	4	—	—	3	—	8	—
4-nucleate " " ?	5	—	—	—	—	—	1	—
6-nucleate " "	1	—	—	—	—	—	—	—
8-nucleate " "	11	—	—	—	—	—	—	—
8-nucleate " " ?	2	—	—	—	—	—	—	—
9-nucleate " "	1	—	—	—	—	—	—	—
Egg and unfused polars	83	—	—	—	—	—	11	—
Egg and unfused polars ?	11	—	—	—	—	—	—	—
Egg and fusing polars	22	—	—	—	—	—	—	—
Egg and fusing polars ?	2	—	—	—	—	—	1	—
Embryo and fusing polars	1	—	—	—	—	—	—	—
Embryo and endosperm	2	—	—	—	—	—	—	—
Embryo and endosperm ?	1	—	—	—	—	—	—	—
Abortive	73	3	—	1	—	4	1	—
Not determined	100	8	4	2	2	17	2	8
Total	636	174	56	135	106	102	53	60

¹ *Townsendia incana* (cultures 6, 17, and 875), *T. Parryi* (cultures 8 and 27), and *T. Rothrockii* (culture 798).

² Explanation of the culture-series symbols will be found in the text, pp. 43-50.

pollen develops in an anomalous manner by the formation of a wall around the four members of the microspore tetrad.

The consequence of much chromosomal pairing in apomictic megasporogenesis probably is sterility. Asexual reproduction is possible only when all or nearly all the chromosomes occur as univalents. One expression of apomictic "meiotic irregularity" as a result of pairing in an apomict is shown in Plate VI, fig. 2. In this photograph of anaphase II, three small groups of dividing chromosomes may be seen in addition to the two main dividing groups. Each of the five groups of chromosomes has its own spindle mechanism. The three small groups of chromosomes would probably have become micronuclei. Both dyads and tetrads with micronuclei have been observed. Such irregularities must often prevent the formation of viable seeds, but the variable chromosome number in this apomictic population suggests that slightly aberrant chromosome races may survive.

The great abundance of dyads in this apomictic form in contrast to their rarity in sexual material (cf. Table IV) is one criterion of apomixis. In addition to the difference in numerical ratio of dyads to tetrads between apomictic and sexual forms, there are considerable morphological differences in the dyads of the two types. The dyad stage of the apomicts is one of long duration during which nuclear-size increase, vacuolation, and a gradual breaking down of the nucellus occur. The dyad stage of the apomicts corresponds to the entire period in sexual forms from the dyad to the early female gametophyte.

The development of dyads directly into two-nucleate embryo sacs was demonstrated by Holmgren (1919) in apomictic forms of two species of *Erigeron*. *Townsendia* apparently is the only other genus in which unreduced female gametophytes are now known to develop regularly in the same manner. It should be noted that the process by which a dyad becomes a two-nucleate embryo sac is a gradual one with no very sharply marked steps. Therefore, assignment of the material at intermediate stages to either the dyad or the two-nucleate categories is sometimes difficult. In this study an arbitrary distinction, based on the condition of the nucellar epidermis, has been made between the two stages. When this structure is intact the material is considered to be at the dyad stage. When the nucellar epidermis disintegrates, the two-nucleate embryo sac stage has been reached.

A few uninucleate embryo sacs have been found in this apomictic form of *T. incana*. They are rare, however, and the present

material is insufficient to permit an interpretation of their significance. Three- and six-nucleate embryo sacs present in this culture could be the result of trisporic embryo sac development. Most of the four-nucleate embryo sacs (Table III) are merely in intermediate stages between two- and eight-nucleate female gametophytes. However, a few are the direct result of tetrasporic development from the megasporule tetrad. A four-nucleate embryo sac of the former type is shown in Plate X, fig. 1. One of the latter type is shown in Plate VIII, fig. 4.

The eight-nucleate stage of the embryo sac is short. The antipodal nuclei disintegrate almost as soon as they are formed. Hence, eight-nucleate embryo sacs are found only at the earliest stages of morphological organization of the female gametophyte.

When the eight-nucleate stage is reached and the antipodals disintegrate, further developmental processes can no longer be designated as the eight-nucleate stage. Only five nuclei, the egg, the two synergids, and the two polars, are involved in subsequent developmental processes. But two major phases are distinguishable during morphological organization of the female gametophyte. Before the polar nuclei have come together, a stage "unfused polars" may be designated (Plate X, figs. 2, 3, and 4 and Tables III and IV). After they have come together, the stage "polars fusing" has been reached (Plate XI, fig. 2 and Tables III and V). Some less conspicuous changes of the egg and synergids occur during the migration and fusing process of the polar nuclei, but these changes are not obvious enough to use in designating developmental stages. In the apomicts the polar fusion process is not completed until after the first division of the egg or a few subsequent nuclear divisions in the proembryo (Plate XI, figs. 3 and 4 and Table VI).

The fairly large amount of abortive and undetermined material in culture 6-I should be noted. This material was fixed after three nights with frost. Freezing may have adverse affects on megasporogenesis and female gametophyte development in apomictic as well as in sexual plants of *T. incana*. Abortion in sexual material, probably caused by freezing weather, was noted previously.

Townsendia incana (culture 6-II). An examination of megasporogenesis in a single plant (6HF) of *T. incana* was made as a check against the other investigations which employed several plants. It is evident from this examination that both "normal" apomictic development and meiotic irregularities indicating features "abnormal" in apomictic reproduction may occur in a single

TABLE IV.
Megasporogenesis in sexual and apomictic populations of *Townsendia*.

Taxon	Culture ¹	Chromo- some no., $2n$	No. of ovules examined	Percentages of ovules with sporogenous tissue at the fol- lowing stages			
				Arche- sporial cells	Dividing megaspore mother cells	Dyads	Tetrads
Sexual							
<i>T. incana</i>	971	18	55	3.6	16.4	1.8	78.2
<i>T. incana</i>	5	18	97	—	7.2	2.1	90.7
<i>T. incana</i>	802	18	58	1.7	19.0	3.5	75.8
<i>T. montana</i> var. <i>montana</i>	35	18	55	1.8	30.9	10.9	56.4
<i>T. grandiflora</i>	39	18	25	—	16.0	4.0	80.0
Apomictic							
<i>T. incana</i>	6-Ia	28	135	—	16.3	77.0	6.7
<i>T. incana</i>	6-II	28	126	8.7	48.5	38.1	4.7
<i>T. incana</i>	6-Va	28	45	—	44.4	55.6	—
<i>T. incana</i>	17-I	ca. 30	119	—	39.5	58.0	2.5
<i>T. incana</i>	875	36	45	4.5	24.5	71.0	—
<i>T. Parryi</i>	8	36	80	2.5	11.3	80.0	7.2
<i>T. Parryi</i>	27	36	15	—	46.7	53.3	—
<i>T. Rothrockii</i>	798	?	52	11.5	50.0	17.3	21.2

¹ Explanation of the culture-series symbols will be found in the text, pp. 28-50.

plant. Diakinesis and metaphase figures were found in which some of the chromosomes were paired, and one metaphase was observed in which all the chromosomes were unpaired. The dyad-tetrad numerical ratio (Table IV) in this plant approximates that of the other plants from culture 6. Micronuclei were found associated with a dyad in one preparation of this material, and the same feature was observed several times in the plants of the mass collection. The study of a single plant suggests, therefore, that all the deviations from the usual apomictic reproductive cycle in the mass collection (culture 6-I) did not come from a single plant. Rather, in this apomictic population, various plants may have irregularities which result primarily from occasional chromosome pairing. Total univalent formation, on the other hand, permits a regular apomictic "meiosis."

Townsendia incana (culture 6-III). The achenes used in this series were from florets in which the corollas had not opened. More advanced florets of the same heads had already reached anthesis. The use of heads with both open and unopen florets made it possible to obtain achenes from florets which would have very soon reached anthesis. The florets which had already opened on these heads were put in the next series to be discussed.

Culture 6-III provides strong direct evidence for apomixis in

Townsendia. A very high proportion of precociously developed embryos were found in the ovules of these florets with unopened corollas (Table V). Some details of early embryo development have been listed in Table VI. These data indicate that the division of the egg ordinarily precedes the completion of the fusion process of the polar nuclei. In angiosperms the division of the primary endosperm nucleus normally occurs before the division of the zygote. This is not true in apomictic *T. incana*. Holmgren (1919) indicated that as far as he could discern, embryo and endosperm development proceeded concurrently in apomictic *Erigeron*. It may be found, however, that the same division sequence, with embryo development before that of the endosperm, will be found to be similar in apomicts of *Erigeron* and *Townsendia*.

When the process of fusion of the polar nuclei is completed the first ensuing division apparently occurs immediately. In this material no completely fused polars, *i.e.*, primary endosperm nuclei, were found. Wall formation in the endosperm probably occurs after the first or second mitotic division series. The nuclear number in the embryo at the earliest stages of development exceeds that of the endosperm, but at slightly later stages the nuclear number of the endosperm is greater than that of the embryo. Very little endosperm remains when the embryo has attained its maximum size. Embryo development appears to be in accordance with the asterad type. The early development of the embryo must be recorded by nuclear number rather than by cell number because wall formation does not always immediately follow mitosis (cf. Plate XII, fig. 3). Mitotic divisions in the young embryo are not synchronous, but those in the early development of the endosperm are. The latter feature is illustrated in Plate XII, fig. 4.

Townsendia incana (culture 6-IV). This series was made from opened florets on the same heads from which unopened florets for the last series were taken. In most of the material at this stage of development the embryos and endosperm had attained a fairly advanced degree of development (Plate XII, fig. 5). The few ovules without embryos and endosperm already developed may have resulted from megasporangia with the reduced chromosome number and probably would have aborted at slightly later stages. The ovules with embryos without endosperm and those with endosperm without embryos were rare and abnormal.

Townsendia incana (culture 6-V). As a check on the reproductive behavior of this apomictic population of *T. incana* in a different environment, material grown in Pullman, Washington and fixed during spring rather than fall growing conditions has

TABLE V.

Classification of ovule development just before anthesis and at or just after anthesis in apomictic populations of two species of *Townsendia*.

Taxon	Culture ¹	No. of embryo sacs examined	Percentages of embryo sacs with the contents listed below				
			Egg and polar fusing	Embryo and polar fusing	Embryo and endosperm	Abortive	Not determined
Just before anthesis							
<i>T. incana</i>	6-III	202	11.9	6.9	68.3	9.9	3.0
<i>T. incana</i>	6-Vb	15	26.6	—	46.8	—	26.6
<i>T. incana</i>	17-II	8	12.5	—	25.0	12.5	50.0
<i>T. condensata</i>	47	32	6.3	3.1	59.3	6.3	25.0
At or just after anthesis							
<i>T. incana</i>	6-IV	144	2.1	1.4	82.6	10.4	3.5
<i>T. incana</i>	6-Vc	22	—	—	90.9	9.1	—

¹ Explanation of the culture-series symbols will be found in the text, pp. 47-51.

TABLE VI.

Comparative developmental stages of embryos and endosperm just before anthesis in apomictic *Townsendia incana*, Culture 6-III.¹

Developmental stage ²	Number observed
2-nucleate embryo and fusing polars	11
4-nucleate embryo and fusing polars	3
2-nucleate embryo and 2-nucleate endosperm	1
4-nucleate embryo and 4-nucleate endosperm	2
4-nucleate embryo and 16-nucleate endosperm	1
5-nucleate embryo and 4-nucleate endosperm	1
7-nucleate embryo and 4-nucleate endosperm	1
8-nucleate embryo and 4-nucleate endosperm	1
Embryo and endosperm at various later stages	131
Total	152

¹ Explanation of the culture-series symbols will be found in the text, p. 47.

² Embryos are listed by nuclear rather than cell number because walls do not always develop immediately after the mitotic divisions.

been utilized. The series was divided into the subseries a, b, and c according to developmental stages. A comparison of the data regarding the material grown in the different environments (culture-series 6-I, 6-II, 6-III, and 6-IV with 6-V in Tables III, IV, and V) suggests that environmental factors cause no significant differences in apomictic reproduction in a single biotype.

Townsendia incana (cultures 17 and 975). Apomictic populations from the northern portion, the southern portion, and about the middle of the range of the species were used in this study to determine what intraspecific variation occurs in apomictic reproduction. A comparison of the data (Tables III and IV) from these different populations of apomictic *T. incana* suggests

that no major and very few minor differences in the apomictic process occur between populations. Culture 17 was divided into two series, I and II, according to developmental stage, for convenience in tabulation.

Townsendia Parryi (cultures 8 and 27). Most of the study of apomixis in *Townsendia* has been made in material with a triploid or triploid-derived chromosome complement, but it was considered essential also to employ some material with the tetraploid chromosome number. Therefore, investigations have been made in two tetraploid populations of *T. Parryi*. The apomictic process in these plants is very similar to that observed in triploid and tetraploid populations of *T. incana*. In *T. Parryi*, as in *T. incana*, the number of univalent chromosomes at diakinesis or metaphase in megasporogenesis is difficult to determine, but numbers approaching 36 may be counted. A double tetrad in one ovule of this material may have resulted from the functioning of two archesporial cells instead of the usual single cell. Some of the integumentary cells in these ovules have a more sporogenous appearance than those in any other *Townsendia* species which has been examined.

Townsendia Rothrockii (culture 798). Microsporogenesis in this population is so irregular that no approximation of the chromosome number has been obtained (seeds for root-tip chromosome counts were not available). Most features of megasporogenesis in these plants are similar to those in apomicts of the other species. However, the dyads and tetrads are somewhat different from those encountered in other material. The dyads are characterized by a wall between the two nuclei. No other population of *Townsendia* is known which has wall formation between the dyad nuclei. Wall formation in the megaspore tetrads of this species also is peculiar. The nuclei of the tetrad have been numbered arbitrarily 1, 2, 3, and 4, in order, proceeding from the micropylar to the chalazal end of the ovule. A single wall has been found in some tetrads between nuclei 1 and 2, in some between 2 and 3, and in some between 3 and 4. In other instances two walls are present, between nuclei 1 and 2 and between 3 and 4. For an apomictic population, the percentage of tetrads formed by these plants is very high. It seems possible that the structures which appear to be tetrads actually are not. Instead, two adjacent archesporial cells may have given rise to dyads and these merely appear to be tetrads because of their adjacent position. More material must be examined before this problem can be satisfactorily solved.

Townsendia condensata (culture 47). A very limited amount of this material was available. The present investigation has demonstrated only that embryos and endosperm are formed in ovules before the corollas open, and evidence of apomixis in the population is thereby obtained.

THE CAUSAL ASPECTS OF APOMIXIS IN TOWNSENDIA

No data on the genetic control of apomixis in *Townsendia* have been obtained. Therefore, the only information on the causes of apomixis in this genus must now come from inference.

The special conditions under which apomixis is expressed in *Townsendia* are suggested by the geographical distribution patterns of the sexual and apomorphic forms. Without exception, the apomicts of *Townsendia* are concentrated at the higher elevations and higher latitudes relative to the total range of the species in which they occur. It seems scarcely deniable that a cold, rigorous climate is a very important factor in permitting the expression of apomixis in *Townsendia*.

A correlation is found in *Townsendia* (as apparently in all groups with apomicts) of the perennial habit and apomixis. This correlation is shown in Chart 1. Gustafsson (1948) and Stebbins (1950) have reviewed the current ideas on the relationship of the perennial habit with polyploidy. Stebbins' interpretation from the available evidence is that the longer growth period of perennials, compared with annuals or biennials, permits a longer time during which a sterility "bottleneck" may be overcome after the initial polyploidization. No experimental attempts have been made to induce apomixis in plants of *Townsendia* by increasing the chromosome number, and it seems futile, therefore, to speculate on the importance of the increase in the chromosome number *per se* in permitting apomixis. However, the lack of correlation of apomixis with hybridization in the genus and the apparently frequent independent recurrence of apomixis in many populations suggest that little more than polyploidy may be required to release the potential apomorphic mechanisms. If apomixis is immediately expressable when the polyploid state has been attained, the perennial habit would hardly be necessary for the prevention of a sterility "bottleneck."

It is generally recognized that the perennial habit, rather than the annual or biennial habit, is correlated with cold, rigorous climates. Apomixis in *Townsendia* also is associated with this type of climate. Perhaps the correlation of apomixis in *Townsendia* with the perennial habit is merely coincidental in that both

features are more or less independently correlated with a cold, rigorous environment. The two features cannot be entirely independent, of course, because apomixis must be of some adaptive advantage to the plants in which it occurs. However, its origin could be merely incidental to the perennial habit. The fact that apomixis occurs in some biennial plants of *Townsendia* as well as in perennial plants supports to some extent this view.

TOWNSENDIA AS AN AGAMIC COMPLEX

From the investigation of Babcock and Stebbins (1938), the agamic complex (a term defined by these authors) in the American species of *Crepis* has become well known. Their work may therefore serve as a standard of comparison for evaluation of the agamic complex in *Townsendia*. Stebbins (1950) has pointed out that from the systematic and phytogeographic points of view, *Crepis* is easier to understand than most of the other known agamic complexes. American *Crepis* is confined to one geographic and climatic zone, and is so recent that the diploid species which gave rise to the polyploids are still growing in the same area. These features are exactly duplicated in *Townsendia*, but similarities extend little farther.

The first difference apparent between the two genera is that their mechanism of apomixis is not the same. Reduction is avoided in *Crepis* by apospory. In *Townsendia* diplospory prevails.

A striking difference apparent between *Crepis* and *Townsendia* is in the role of hybridization with apomixis. In *Crepis*, Babcock and Stebbins (1938, p. 45) state: ". . . these diploids are completely distinct from one another in their morphological characteristics, and are completely isolated from one another genetically." The experimental and comparative morphological studies in *Townsendia* clearly indicate that diploid, sexual plants of several of the species of *Townsendia* will hybridize and possibly no great reduction in the fertility of the hybrids results.

In *Townsendia* it appears that hybridization may occur entirely independent of polyploidy. No polyploid system is necessary to permit the exchange of genes between the species. Likewise, in *Townsendia* hybridization seems to be an entirely unnecessary feature for setting in action apomictic reproduction. In spite of frequent hybridization between the diploid forms of the species of *Townsendia* there are as many, if not more, suspected populations of autoploid apomicts as allopolloid apomicts. All of the presently known apomicts of *T. Rothrockii*, *T. scapigera*,

T. strigosa, and *T. grandiflora* are apparently autoploid. *Townsendia Parryi* and *T. Hookeri* have a very high percentage of autoploid apomicts, and even *T. leptotes*, *T. exscapa*, and *T. montana* seem to have numerous autoploid apomicts. In none of the species do all of the apomicts appear to be allopolloid. Thus, apomixis in *Townsendia*, apparently unlike that in *Crepis*, can be viewed independently from hybridization. The only reason that hybridization appears to be involved in the apomicts of *Townsendia* is because some of the diploid, hybrid-derived types have become polyploid apomicts. Probably some of the gene recombinations which result from hybridization are more vigorous than the non-hybrid types, and when these are fixed by apomixis they have an advantage over the non-hybrid types and thus become widespread. Otherwise, hybrid apomicts in *Townsendia* might not even be known.

Another strongly contrasting feature between the apomicts of *Crepis* and those of *Townsendia* is that some of the sexual forms of *Townsendia* which have apomixis are definitely not relict types. Stebbins (1950, p. 400, in quoting Gustafsson's characterization of *Hieracium* and *Taraxacum*) has indicated that five of the seven species of *Crepis* are "depauperate and relict." In only four taxa of *Townsendia*, *T. condensata*, *T. montana*, var. *montana*, *T. Parryi*, and *T. Rothrockii*, do the sexual forms have a very limited and possibly relict distribution. Even *T. Parryi* probably should not be included in the above group because its sexual forms have both a considerable geographic range and interpopulation variability. In the other species of *Townsendia* which have apomixis, the sexual forms have much morphological diversity and often are nearly as widespread as, or even more widespread than, the apomictic forms. Thus, even though the American species of *Crepis* are similar to the species of *Townsendia* in occupying a single geographic and climatic realm, and in having the sexual precursors of all the species known, the two agamic complexes have few other common features.

A limited evolutionary future for the apomicts of *Townsendia* may be postulated, as the embryological data indicate that apomixis is obligate in the genus. The statement by Stebbins (1950, p. 417) that agamic complexes are "blind alleys" is probably better applicable to the *Townsendia* apomicts than to the facultative apomicts of many other genera.

The best evidence that the apomicts of *Townsendia* have not given rise to any new apomictic forms lies in the fact that no species of the genus is represented only by apomictic types. Sex-

ual precursors of all the apomictic forms are known, which is positive evidence that the apomicts have undergone little if any evolution.

Although their evolutionary future may be limited, the success of the apomicts in colonizing wide areas is evident. Apomixis occurs in 12 of the 21 species of *Townsendia*; it occurs abundantly in nine species. The geographic range of the apomicts in some of these species exceeds considerably that of the sexual forms. Therefore, apomixis must have potent adaptive advantages.

TRENDS OF EVOLUTION

DIVERGENT EVOLUTION

The patterns of speciation in *Townsendia* seem explainable mainly on a geographic, climatic, and edaphic basis. A correlation of the morphological traits of the taxa of *Townsendia* with their geographic distributional-patterns makes possible a suggestion of their phylogenetic relationship. A tentative phylogenetic diagram is presented in Chart 1. The center of this diagram may be imagined as the time when diversification in *Townsendia* began.



CHART 1. Phylogenetic relationships of the species of *Townsendia* and a summary of the habit and the presence of apomixis in the species.

The present time level is indicated by the terminations of the various lines at the species names. The length of separation of each line from the others is intended to suggest the relative amount of morphological divergence which each species has developed from the others. At the periphery of the diagram the species have been placed, in so far as feasible, closest to the species which their development parallels. The broken line through the center of the figure separates the caulescent from



MAP 1. Phylogenetic relationships of the species of *Townsendia* on a geographic basis.

the acaulescent types. The relative amount of apomixis in the various species has been indicated.

The phylogenetic relationships of the species on a geographic basis are suggested by Map 1. The arrow-points indicate derived species, and where there are no arrows terminating the lines, the possible derivations are not suggested. The broken lines indicate indistinct relationships between more primitive types.

The extensive climatic variations of the Pleistocene must be acknowledged as important factors in the phylogenetic history of *Townsendia*. It seems probable that some of the species as they are now known were not in existence during much of the Pleistocene. The high level of correlation of some species with specialized edaphic and climatic conditions suggests that climatic changes could have easily taken their toll of various evolutionary experiments. On the other hand, the relative abundance of *Townsendia* species now in habitats which were unavailable during the last glacial advance could indicate both the recent evolution of some new types and the ability for rapid migration of some of the older forms.

An understanding of the evolutionary trends in *Townsendia* requires an understanding of the primitive characteristics in the genus. *Townsendia formosa* seems to qualify in all respects as the most primitive member. The probable primitive generic characters are outlined in the section on generic relationships.

The species with the greatest morphological similarity to *T. formosa* is *T. eximia*. The latter species most conspicuously differs from the former in having a shorter life-span, in developing a branched stem, and in having a taproot rather than a fibrous-root system. These species occur allopatrically in adjacent mountain masses mostly in New Mexico. *Townsendia eximia* has close relatives on all geographic sides of its range. To the east and north, respectively, are the very close cognates *T. texensis* and *T. grandiflora*. *Townsendia glabella*, which occurs only a short distance to the northwest, is similarly closely related to *T. eximia*.

A continuation of the reduction trend which has produced *T. glabella* is found a short distance to the north in *T. leptotes*. These two species occur together in southwestern Colorado, but *T. leptotes* is more diversified to the north of the range of *T. glabella*. Differentiation through isolation probably occurred while the two populations were isolated from each other by the mountain masses in western Colorado, and the populations of *T. leptotes* within the range of *T. glabella* in southwestern Colorado are probably recent migrants there.

Populations of the *T. leptotes* type which migrated to the east side of the Rocky Mountains in Colorado have been geographically isolated there and the resulting evolutionary divergence has produced *T. Hookeri*. Both of these species are advanced types; one obvious feature indicating their advanced nature is the extreme reduction of the aerial portions of the plant body. It should be noted that the sexual forms of *T. Hookeri* and *T. leptotes* are entirely allopatric, but the apomicts of *T. Hookeri* occur in the range of the sexual forms of *T. leptotes*. The apomicts of both species have wide geographic ranges.

Speciation from the *T. eximia-T. glabella* stock can also be traced geographically to the west of the range of that evolutionary complex. *Townsендia montana* (both varieties) exhibits a fairly close morphological relationship to the *T. eximia-T. glabella* stock and probably has resulted after geographical isolation in the mountainous areas of central and north-central Utah. Differentiation may have occurred in isolated populations at both high and low elevations; the high-elevation type has become *T. montana*, while evolution in the populations at lower elevations has resulted in *T. mensana*.

The evolutionary trends in specialization from a more generalized *T. eximia* stock have occurred in the mountainous areas to the northeast, north, and northwest of the range of *T. eximia*. Such a pattern is probably attributable mostly to the fact that a large number of habitats suitable for occupancy by *Townsендia* populations occur in that area. Because of the mountainous terrain, the populations were easily isolated from each other, and climatic changes probably have facilitated the isolation. The divergences apparently have been recent enough that the morphological trends they followed are still evident. Many connecting "links" may not yet have become extinct in spite of numerous Pleistocene climatic fluctuations.

Speciation with a different geographic pattern from that outlined above has had an orientation from the northern rather than from the southern limits of the diversity of the genus. The most primitive member of the northern complex is *T. Parryi*. One clear trend of specialization away from that species involves *T. florifer* and *T. scapigera*. The stock which has given rise to *T. florifer* apparently became adapted to the arid conditions of the Snake River plains and spread from there to the south and west. *Townsендia scapigera* is apparently a recent segregant from plants in the western portion of the range of *T. florifer*. From the very different climatic conditions which must have prevailed during

the last ice advance in the area which *T. florifer* and *T. scapigera* now occupy, it must be inferred that these two species have had a recent origin. *Townsendia Parryi*, their closest relative, is in a geographic position which further indicates that this evolution must have been recent. The geographic trend in evolutionary specialization along this line is from the northeast in Montana to the southwest in Nevada. It can best be interpreted as a morphological reduction series which occurred only in one direction. The advanced forms probably have spread since the last glaciation into more arid regions from an area relatively near the present range of *T. Parryi*.

A different evolutionary trend from *T. Parryi* stock appears to have occurred in a southeastern direction from the present range of that species. *Townsendia condensata* and *T. spathulata* are the specialized members along this line of development. They appear to have become strongly adapted to some of the peculiar edaphic situations of western Wyoming. *Townsendia condensata* may be a relict type of a former colder and more moist period, and it is now represented mostly by alpine apomicts. Edaphically, *T. spathulata* is one of the most highly specialized species of *Townsendia*. Its unusual habitat requirements probably are a reflection of its reduced morphological features. Very likely it could not withstand the competition from larger plants on sites more than sparsely vegetated.

Part of the evolutionary line which may have diverged from a *T. Parryi* prototype is not so closely related to that complex as the two trends just outlined. However, the ancestral forms which gave rise to *T. strigosa* and *T. incana* probably occupied the Colorado Plateau and Green River basin area and may have been somewhat similar to *T. Parryi*. The *T. strigosa-T. incana* stock probably migrated into the central highlands of Mexico and, with isolation, *T. mexicana* has arisen. The separation of *T. strigosa* and *T. annua* into distinct taxa appears to have been a recent occurrence. *Townsendia incana* and *T. Fendleri* similarly are cognate species.

The clearest patterns of speciation in *Townsendia* indicate that geographic isolation has been of prime importance in the evolution of the members of the genus. A position of importance for polyploidy in the evolutional pattern seems to be ruled out, as no polyploid sexually reproducing species are known to exist. The role of hybridization in the development of new forms in *Townsendia* seems relatively unimportant, but the process does occur and cannot be entirely excluded as a possible evolutionary

agent. However, none of the present species is suspected to be of hybrid origin.

The importance of geographic isolation in speciation in *Townsendia* is further emphasized by the unique case of *T. exscapa*. It is pointed out in greater detail in the systematic treatment that this species occurs in an area where Pleistocene climatic fluctuations probably would not break up its range into geographically isolated populations. *Townsendia exscapa* has therefore not become differentiated into segregate species but rather is a single large species showing clinal variation.

From both the negative approach (with *T. exscapa*) and the positive approach (with the other species), the role of geographic isolation in the development of the species of *Townsendia* is striking. Other factors, such as polyploidy and hybridization, may be important evolutional factors after a group has become somewhat differentiated through geographic isolation. In the young and actively evolving species of *Townsendia* the primary importance of geographic isolation in permitting the fixation of independent gene mutations seems amply clear.

CONVERGENT EVOLUTION

Convergent or parallel evolution is a feature of some of the species of *Townsendia*. This phenomenon is forcefully illustrated by mixed collections which are often unwittingly made by collectors when two species grow side by side. For example, the apomictic plants of *T. montana* var. *montana* and those of *T. leptotes* which occur in the high mountains of northern Utah and north-central Idaho are so similar that they have been confused in the field by five collectors (including myself). A careful examination of the plants and a knowledge of the total range of variation to be expected in each of the species made it possible to show that two specific elements were involved.

Perhaps the instance of convergent evolution in *Townsendia* which has misled the most botanists is between *T. exscapa* and *T. Hookeri*. When Hooker established the genus he did not realize that his material included two species. Ninety-three years later Larsen (1927) first recognized that Hooker had based his "species" on two different specific elements. Specimens from the central portions of the ranges of the sexual forms of these species are easily distinguishable.

In the cases of parallel evolution in *T. montana* and *T. leptotes* and in *T. exscapa* and *T. Hookeri*, hybridization may have been the factor which permitted convergent evolution. Strong selec-

tive forces in the rigorous habitats these plants occupy probably permitted only a very limited number of morphological (and physiological) recombinants to survive. These happened to be nearly intermediate forms between the two species. Successful recombinations between the species are now fixed by apomixis.

An instance of convergent evolution which has probably involved hybridization but not apomixis is found between *T. Fendleri* and *T. annua*. These species were similar enough that Larsen was confused and treated them as a single species in her revision of the genus. A mixed collection of the two species has occurred at least once (cf. discussion of *T. Fendleri* in the systematic treatment).

Two cases of convergent evolution which appear not to have involved hybridization are between *T. mensana* var. *Jonesii* and *T. scapigera* on the one hand and *T. mensana* var. *mensana* and *T. Hookeri* on the other. In the former case, the populations of *T. mensana* var. *Jonesii* in the Charleston Mountains of Nevada are superficially very similar to some of the plants of *T. scapigera* in the Inyo Mountains of California. There is no evidence that these populations of the two species have ever hybridized. Rather, it seems probable that the very similar climatic regimes in the two areas have been responsible for the selection of life-forms which have a considerable degree of morphological similarity. One is led to assume that the genetic complement of the genus is such that it will permit the expression of only a limited number of morphological types under a given set of environmental conditions.

In the case of the convergent evolution of *T. mensana* var. *mensana* and *T. Hookeri*, the possibility of hybridization seems to be very clearly ruled out. In the Uinta Basin of Utah where this convergence occurs, the population of *T. Hookeri* is apomictic. Sexual forms of *T. Hookeri* are known only on the eastern side of the Rocky Mountains and it seems probable that the population of this species in the Uinta Basin migrated there as an apomict (this postulate is given fuller consideration under the discussion of *T. Hookeri* in the systematic treatment). These apomictic plants have been able to survive because their basic genotype was already suited for the cold winters and dry summers and peculiar edaphic conditions which occur in the Uinta Basin. The narrowly endemic *T. mensana* var. *mensana*, in contrast, is a sexual form which apparently has developed under the influence of the factors of natural selection in the Uinta Basin. The similar-

ity of *T. Hookeri* and *T. mensana* is sufficient that Larsen (surely on a superficial basis) considered them to be a single species.

It seems unlikely that the convergent evolution which has been outlined above could be important in progressive speciation in *Townsendia*. However, its frequent occurrence gives a strong indication of the great genetic plasticity of the species of *Townsendia* under the action of diverse environmental forces. This plasticity must have made possible the rapid divergent evolution in *Townsendia*.

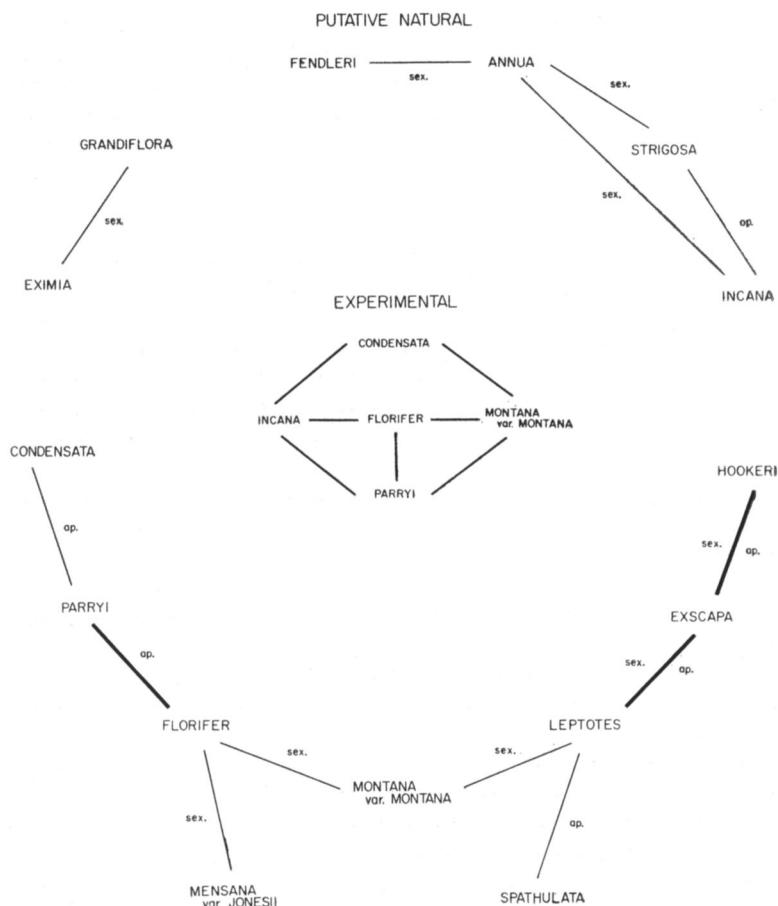
HYBRIDIZATION

Experimental F_1 hybrids have been obtained between the seven species of *Townsendia* which are indicated on Chart 2. All crosses attempted were successful. One plant of the cross *T. florifer* \times *T. incana* and one of the reciprocal were grown to maturity. These had neither meiotic irregularities nor a greatly reduced pollen fertility (cf. Beaman, 1954). Conditions at the time the F_1 plants were available did not permit securing the F_2 crosses, so none have been made. Plants of the other F_1 crosses were grown for some time under greenhouse conditions in Cambridge, Massachusetts, but growth of both hybrids and non-hybrids was unsatisfactory. From the few crosses which have been obtained, it appears that genetic barriers are lacking between those species involved, but further experimental evidence is needed.

Most of the crosses attempted were between relatively closely related species (compare experimental crosses, Chart 2, with phylogenetic relationships, Chart 1). A greater number of crossing attempts, with special emphasis on obtaining hybrids between the more distantly related species, is contemplated as a future project. Such crosses might provide evidence in addition to that of comparative morphology for inferring evolutionary relationships. Also, extensive crossing experiments could provide important data on the nature of genetic barriers between species. With a closely related series of species, such as those of *Townsendia*, it might be possible to correlate levels of morphological differentiation with the development of genetic isolating mechanisms. Thus a better insight might be gained on the nature of this important factor in speciation.

Evidence for natural interspecific hybridization has been outlined in the systematic treatment under the discussions of the species. The species between which natural hybridization is sus-

HYBRIDIZATION IN TOWNSENDIA

CHART 2. Hybridization in *Townsendia*

pected are indicated on Chart 2. Putative hybrids from sexual populations are indicated by the symbol "sex." and those from apomictic populations by the symbol "ap.". Species in which hybridization seems frequent, based on examination of herbarium material, are connected by heavy lines, and those which appear to hybridize only infrequently are connected by narrow lines.

In a genus with 21 species it seems unusual that 15 of its mem-

bers should be involved in hybridization. To understand the basis of this peculiarity, it is natural to inquire why the other species are not involved also. Hybridization is not known in *T. formosa*, *T. glabella*, *T. mexicana*, *T. Rothrockii*, *T. scapigera*, and *T. texensis*. Most of these species are geographically isolated from all the other species. *Townsендia glabella* and *T. scapigera* are the only two members of this group which, on a geographic basis, might be suspected of being involved in hybridization with other species. Neither of these is well enough known to permit a sufficient understanding of its population diversity. The distribution of natural hybridization among the species suggests that the principal requirements for its occurrence are an overlapping or adjoining of ranges of the species and a coincidence of flowering time.

Sexual hybrids occur in a greater number of species than do hybrids in which apomixis is involved (Chart 2). From their distribution within the species, it appears that in *Townsендia* hybridization and apomixis are independent phenomena. Hybridization probably is not necessary to permit the expression of apomixis. However, certain hybrid derivatives which become apomictic probably have a greater survival value than some non-hybrid apomicts.

It seems probable that in *Townsендia* hybridization is not a function of intermediate edaphic conditions. Most of the species which occur together have similar, rather specialized, edaphic requirements. Thus it appears that soil conditions figure principally in permitting species to grow together where they can hybridize.

Although hybridization occurs in numerous species, there is little or no evidence to indicate that it is an important factor in speciation in *Townsендia*. It seems mainly to have increased the morphological diversity of certain species where it is coupled with apomixis. Sexual hybrids are most abundant between *T. exscapa* and *T. Hookeri*, and may be abundant between *T. florifer* and *T. mensana* var. *Jonesii*. Otherwise they are not frequently encountered. The diversity in the species as a result of hybridization seems slight in comparison to that which has resulted from geographic isolation.

MORPHOLOGY

Townsендia is similar to many other genera of the *Compositae* in that its members have considerable microscopic homogeneity. Gross morphology is more useful than minute structure in deter-

mining specific limits. Proper determination of the taxa usually must be based on several characters from various aspects of the plant.

One species of *Townsendia* has been the subject of an anatomical study by Bunton (1910). Her investigation was directed at determining in *T. exscapa* the anatomical adaptations to xerophytism.

HABIT. Two trends occur in the genus in the modification of the habit. Erect, monocephalous stems and a rhizomatous basal mat, a primitive and unspecialized habit, are found only in *T. formosa*. One reduction trend has resulted in low, densely rosulate, matted or tufted perennials, as in *T. Hookeri*. Another trend involves less shortening of the stem, but the life-span of the plant is reduced, as in *T. annua*.

ROOTS. All but one of the species of *Townsendia* have taproots; the exception is *T. formosa* which has a fibrous root-system. The taproots of young plants are slender and light in color; in older plants they become thick and woody but never develop a thick, rough bark. A gradual transition zone is usually found between the root and stem, and leaf-scars best indicate the change from root to stem. The biennials are characterized by an enlarged root-stem junction which seems to develop during the rosette stage of the first year of growth; this swollen portion may be hollow or have a chambered pith.

STEMS. The perennial species usually have a branched, woody caudex which forms a crown at the ground surface. Herbaceous stems may develop from the caudex branches, as in *T. glabella*, or they may be terminated only by tufts of leaves and flowering heads, as in *T. Hookeri*. The caudex branches of the short-lived perennials are slender; those of the longer-lived species become correspondingly thicker. In most of the species, the stem is expanded just below its junction with the head. This condition is seen most clearly in *T. Parryi*. Some members of the genera closely related to *Townsendia* exhibit the same feature. A few of the species of *Townsendia* are characterized by peduncles, but this character is not prevalent in the genus. Usually the heads terminate more or less leafy stems.

LEAVES. External leaf morphology in *Townsendia* is remarkably uniform. Throughout the genus leaf modifications are minor ones in shape, pubescence, and texture. The insertion is alternate and there is no strong differentiation between blade and petiole. The leaves are expanded at the junction with the stem, narrowed into a petiole-like portion, and expanded again into the blade.

With but two minor exceptions, the margins are always entire. Two minute notches infrequently occur at the apices of the leaves of *T. Parryi*, and in *T. mexicana* one or two small lobes are sometimes found near the apices. In the acaulescent species all the leaves on a single plant are essentially the same size and shape. Caulescent plants have a basal rosette of leaves longer and broader than those of the upper portions of the stem. There is little differentiation between upper and lower leaf surfaces in any of the species. Thickened leaves are found mostly in plants growing at moderate to high altitudes, as in *T. Rothrockii*, but some species frequenting the higher elevations do not have thickened leaves. Involute leaves occur primarily in the narrow-leaved forms.

PUBESCENCE. Both the stems and foliage in the members of *Townsendia* are characterized by a strigose pubescence. The trichomes are usually few-celled (3-8) and have a somewhat enlarged basal portion and a sharp-pointed apex. Taxonomically, the most useful pubescence variation is in density. Excluding the acheneal hairs, there are only two variations in trichomes in the genus which are not merely quantitative. Simple, multicellular trichomes, conspicuous because of their very short cells, are found on the upper portion of the stem in *T. formosa*. In *T. condensata* and *T. spathulata* the trichomes are very long, with elongate cells which have conspicuous end walls; these trichomes may be very abundant, giving the plant a woolly aspect.

The phyllaries may be strigose, pilose-strigose, or glabrous. In several species the trichomes of the phyllaries tend not to be appressed in a single, apical direction while stem and leaf trichomes almost invariably are apically appressed.

INVOLUCRE AND RECEPTACLE. Generally, the involucre in *Townsendia* is hemispheric or campanulate, but in *T. montana* and *T. mensana* it may be somewhat obconical.

Phyllary morphology comprises a useful set of taxonomic criteria in the genus. In addition to the number of series in which the phyllaries occur, overall phyllary shape, form of the apex, and nature of the margin are useful characters. In species with very broad phyllaries, the apices tend to be obtuse, while in those with narrower phyllaries, the apices are acute, but acuminate apices occur both in species with wide and with narrow phyllaries. Only two species, *T. eximia* and *T. grandiflora*, are characterized by conspicuously bristly phyllaries. The margins always are at least somewhat scariosus and ciliate or lacerate-ciliate and may serve as a useful character to someone familiar with the group,

but characters of the margin are too intangible to be useful in the key.

Characteristics of the receptacle have proved useful primarily in the demonstration of the generic relationships of *Townsendia*. A conical receptacle is found only in *T. formosa*, the most primitive member of the genus; all the other species have nearly flat or slightly convex receptacles. The close generic relatives of *Townsendia* have conical receptacles.

FLOWERS. The pistillate ray-florets occur in a single series. As is characteristic in the heterochromous members of the *Astereae*, the species of *Townsendia* have only cyanic pigments in the ray-corollas, and ray color is often a useful taxonomic character. Uniformly blue or bluish-purple rays occur in four species and in some populations of two others. In most of the members of the genus, the rays are white on the adaxial surface and have a darker abaxial surface, often with a median stripe which may be pinkish, lavender, or mauve-purple. In old or dried rays the color usually is darker. The adaxial surface of the ray-corollas is generally glabrous, but the abaxial surface in several species is beset with few to numerous gland-like hairs, which apparently are under the control of very few genes. Care must be observed in their taxonomic use, but they are a constant feature of a few species. The length of the ray-corollas is sometimes helpful in delimiting species. The width, on the other hand is of little use. In some of the apomicts the rays never fully expand.

The only character of the disk-corollas which has been used in this study is their length. A comparison of the length of the pappus to that of the disk-corollas has been helpful in several instances.

The style-branches of *Townsendia* are typical for a member of the *Astereae*. The disk-styles have the upper portion of the branches modified with projecting hairlike cells, while the ray-styles have marginal stigmatic surfaces extending nearly to the apices of the branches. There are slight differences in shape of the style-branches between some of the species, but these are of no use for distinguishing closely related or nearly similar species.

Neither anther structure nor morphological characteristics of the pollen has been employed as taxonomic criteria in this investigation. However, pollen studies have been of great value in distinguishing specimens from sexual populations from those representing apomictic populations. The peculiarities of pollen formation in the apomicts are considered in the section on reproduction. Pollen of the sexual plants (see Plate IV, fig. 1) is

spherical, three-pored, and uniformly spinescent. It is three-nucellate at anthesis. At maturity its mean diameter ranges between 23 and 30 microns.

ACHENES AND PAPPUS. There is considerable diversity in size and shape of the achenes of the species of *Townsendia*. Within the species the achenial morphology is relatively uniform, and in some instances provides useful taxonomic characters. Among the more problematical species the achenes are so similar that they are of little systematic value. Achene shape varies from narrowly oblanceolate to obovate, and the achenes are always somewhat compressed. They usually have ribbed or callous-thickened margins.

Gray (1880) in his synopsis of the genus placed considerable reliance on the achenial hairs in delimiting species and groups of species. In the present study also the character of these hairs has been found useful. Macloskie (1883) examined the achenial hairs of all the species of *Townsendia* known at the time of his study, and the descriptive terms which he and Gray used have been employed in this paper. The achenial hairs are always duplex; two connate cells project from the surface of the achene. One cell originates at the surface of the achene, while the other joins an enlarged or unenlarged basal cell. A second basal cell might occasionally be present but apparently is mostly reduced or absent. The distal portions of the two principal cells may remain connate and be acutely terminated or one cell may exceed the other and have an acute apex. Hairs with acute apices are termed "entire" in this treatment. Hitchcock and Thompson (1945) noted that the hairs of *T. condensata* (called *T. spathulata* in their paper) are simple. However, the duplex condition is retained in the hairs of this species, and the term "simple" is misleading. In some species of *Townsendia* the achenial hairs are bifurcate or emarginate, but glochidiate hairs are commonest in the genus. In the latter type, the distal ends of the two elongate cells are separate and recurved. There is no evidence in *Townsendia* of a glandular nature of the achenial hairs.

The pappus has been a much-used taxonomic character, and within limits it has great value. It cannot be used, however, to the exclusion of other characters for distinguishing species. The pappus is always uniserial and is made up of connate setae which are usually arranged in well-developed, rather stiff bristles. At frequent (sometimes very frequent) intervals along the bristles, individual setae project out as non-recurved or rarely recurved barbs or barbulae. In *T. exscapa* the bristles may reach a length

of 13 mm. while in *T. formosa* the longest never attain a length of 1.5 mm. The pappus of *T. eximia* usually consists of two bristles and a crown of squamellae, but as many as 50 bristles are found in *T. exscapa*. The ray-pappus of several species is much shorter than the disk-pappus; the former sometimes is so short that the connate setae merely form a ring of coroniform squamellae around the apex of the achene. The short ray-pappus is a constant feature in some species but mostly there are exceptions which make it an unreliable character. In *T. mexicana* the ray-pappus appears to have been reduced mostly to single, separate setae which frequently are somewhat glochidiate, resembling the achenial hairs.

MEASUREMENTS. In this study the measurements have been based on dried material. Boiling was employed only in the width measurements of the ray-corollas. Small objects, such as phyllaries, were measured under 9 \times magnification with a millimeter rule. Very small parts, such as ray-pappus squamellae, were measured with the same rule under 54 \times magnification. Pollen measurements were obtained with a compound microscope and a calibrated ocular micrometer.

SYSTEMATIC TREATMENT

In the citation of specimens, herbarium abbreviations in the third edition of "Index Herbariorum" (Lanjouw and Stafleu, 1956) have been used. These herbaria and their abbreviations are: National Museum of Canada (CAN); California Academy of Sciences (CAS); University of Colorado (COLO); Carnegie Museum (CM); Colorado A. and M. College (CS); Science Service, Department of Agriculture, Canada (DAO); Dudley Herbarium of Stanford University (DS); Chicago Natural History Museum (F); Gray Herbarium (GH); University of Illinois (ILL); Idaho State College (IDS); Herbarium, Royal Botanic Gardens, Kew (K); Herbario Nacional del Instituto de Biología de la Universidad Nacional de México (MEXU); University of Michigan (MICH); Missouri Botanical Garden (MO); Montana State College (MONT); Montana State University (MONTU); Michigan State University (MSC); United States National Arboretum (NA); University of Notre Dame (ND); New York Botanical Garden (NY); Oberlin College (OC); Bebb Herbarium of the University of Oklahoma (OKL); Philadelphia Academy of Natural Sciences (PH); Pomona College (POM); Rocky Mountain Herbarium, University of Wyoming (RM); Rancho Santa Ana Botanic Garden (RSA); Sul Ross State College (SRSC); University of California (UC); National Museum, Smithsonian Institution (US); University of Utah (UT); Intermountain Herbarium of the Utah State University (UTC); University of Wisconsin (WIS); State College of Washington (WS); University

of Washington (WTU); Yale University (YU). Approximately 4500 specimens were examined in this study.

The symbol "*" before an herbarium abbreviation signifies that pollen from that specimen is characteristic for sexually reproducing, diploid plants; the symbol "†" signifies that pollen from that specimen is characteristic for apomictic, polyploid plants (in some cases no pollen was produced). The symbol "*?" signifies that the specimen probably represents a sexual, diploid population, but the advanced flowering stage did not permit a positive determination.

Townsendia Hook. Fl. Bor.-Am. 2: 16. 1834.

Annual, or most frequently biennial or perennial, caulescent or acaulescent herbs with taproots (fibrous-rooted in one perennial species); erect, suberect, decumbent, or rosulate; leaves alternate, spatulate to linear, entire or rarely lobed or toothed, glabrate to densely pubescent; indument of simple, few- to many-celled, mostly appressed trichomes; heads pedunculate or terminal on stems or sessile and submerged in tufts of leaves, large or small and correspondingly few- to many-flowered; receptacle convex, rarely conical, areolate, minutely pubescent; phyllaries imbricate, in 2-7 series, obovate-ovate to linear-subulate, usually scarious-ciliate margined; ray-florets pistillate, fertile, unisexual, ca. 10-100, mostly 20-40; ray-corollas broadly linear to oblong-linear, uniformly blue, or whitish to pink (rarely dull red or lavender) on the adaxial surface and darker on the abaxial surface, often with a median pink to lavender stripe, inconspicuously 2-3-toothed, glabrous or glandular mostly on the abaxial surface; disk-florets hermaphroditic, more or less numerous; disk-corollas yellow and frequently pink- or purple-tipped or tinged, glabrous or lightly glandular; style-branches lanceolate, oblanceolate or oblong-linear, 0.8-2.5 mm. long, the upper portion (shorter or absent in the rays) with elongate, hair-like cells, the lower stigmatic margins minutely and densely papillose; disk-styles elongating at anthesis, serving as pollen-disseminators; achenes oblanceolate to obovate, compressed, 2-ribbed, those of the ray sometimes 3-ribbed, glabrate or most frequently pubescent with duplex hairs, the hairs with glochidiate, bifurcate, emarginate or entire apices, achenes sometimes papillose; disk-pappus unisexual, of few to numerous subulate or acicular, terete or obcompressed, plurisetose, barbellate bristles (rarely of very short bristles and squamellae less than 1.5 mm. long); ray-pappus similar to that of the disk, or variously shortened, sometimes to a mere crown of connate or semi-connate, short bristles or squamellae (rarely reduced to glochidiate setae). Type-species (originally the only species): *Townsendia exscapa* (Richards.) Porter.

ARTIFICIAL KEY TO THE SPECIES AND VARIETIES

- A. Disk-pappus of very short bristles and squamellae less than 1.5 mm. long; plants fibrous-rooted and rhizomatous or stoloniferous; receptacle

- conical 1. *T. formosa*.
- A. Disk-pappus of bristles longer than 2 mm. (rarely with squamellae or short bristles also); plants taprooted, not rhizomatous or stoloniferous; receptacle merely convex or flat B.
- B. Disk-pappus of short squamellae or bristles and 2-4 (rarely up to 8) longer, coarse bristles 2. *T. eximia*.
- B. Disk-pappus of 12 or more plurisetose bristles C.
- C. Phyllaries bristly-stiff, apices attenuate-acuminate 3. *T. grandiflora*.
- C. Phyllaries not bristly-stiff, apices acuminate, acute, or obtuse D.
- D. Achenes at or near maturity with readily deciduous pappus; plants villous-woolly with long trichomes E.
- E. Phyllaries acuminate; involucres of largest heads more than 17 mm. wide 15. *T. condensata*.
- E. Phyllaries acute; involucres of all heads less than 16 mm. wide 16. *T. spathulata*.
- D. Achenes with persistent pappus; plants not villous-woolly F.
- F. Acheneal hairs bifurcate or unevenly forked with one prong exceeding the other (sometimes appearing simple), not glochidiate by recurved prongs G.
- G. Plants rosulate or cespitose-acaulaceous; heads pedunculate or sessile among the tufts of leaves H.
- H. Ray-corollas glabrous or lightly glandular on the abaxial surface; achenes with delicate tangled hairs near the base 7b. *T. montana* var. *minima*.
- H. Ray-corollas densely glandular on the abaxial surface; achenes pubescent from base to apex with straight or nearly straight hairs I.
- I. Phyllaries in 3 (rarely 4) series, acute, pilose-strigose on the outer surface 14. *T. scapigera*.
- I. Phyllaries in 4 (rarely 5) series, obtuse or acute, nearly glabrous or the outer lightly pilose-strigose near the apex 8b. *T. mensana* var. *Jonesii*.
- G. Plants with erect or spreading-suberect stems; heads terminating leafy stems J.
- J. Rays blue (rarely whitish or pinkish); phyllaries acuminate, in 4-7 (mostly 5) series 12. *T. Parryi*.
- J. Rays white or pinkish; phyllaries acute, in 3-4 (rarely 2) series 13. *T. florifer*.
- F. Acheneal hairs glochidiate or achenes glabrous K.
- K. Phyllaries linear to narrowly lanceolate (broader in some plants with the disk-corollas longer than 6 mm. and in some plants with very narrow, glabrous leaves), apices acuminate or acute, in 5-7 series L.
- L. Phyllaries with a tuft of tangled cilia at the apex, linear, acuminate 10. *T. Hookeri*.
- L. Phyllaries without a tuft of tangled cilia at the apex, narrowly lanceolate, acute M.
- M. Disk-pappus more than 6.5 mm. long; leaf mid-veins usually conspicuous 11. *T. exscapa*.
- M. Disk-pappus less than 6.5 mm. long (if longer, the

- ray-pappus less than half the length of the disk-pappus); leaf mid-veins not conspicuous N.
- N. Leaf bases densely woolly-pubescent with long trichomes 8a. *T. mensana* var. *mensana*.
- N. Leaf bases glabrous or only lightly pubescent 9. *T. leptotes*.
- K. Phyllaries broadly lanceolate to ovate or elliptic, apices obtuse or acute, in 2-5 series O.
- O. Leaves or achenes or both glabrate P.
- P. Ray-pappus nearly as long as the disk-pappus 7a. *T. montana* var. *montana*.
- P. Ray-pappus less than $\frac{1}{2}$ as long as the disk-pappus Q.
- Q. Leaves conspicuously thickened; heads nearly sessile or short-pedunculate; phyllaries obovate, ovate, or broadly oblanceolate, mostly obtuse 6. *T. Rothrockii*.
- Q. Leaves not conspicuously thickened; heads long-pedunculate; phyllaries lanceolate, acute 5. *T. glabella*.
- O. Leaves and achenes conspicuously pubescent R.
- R. Disk-pappus shorter than the disk-corollas S.
- S. Phyllaries in 2 series; plants of Mexico 21. *T. mexicana*.
- S. Phyllaries in 3-4 series; plants of the United States T.
- T. Plants annual; phyllaries mostly in 3 series, the apices obtuse 20. *T. annua*.
- T. Plants perennial; phyllaries mostly in 4 series, the apices acute 18. *T. Fendleri*.
- R. Disk-pappus as long as or longer than the disk-corollas U.
- U. Caudal biennials or short-lived perennials V.
- V. Ray-corollas blue; plants of the Texas Panhandle and western Oklahoma 4. *T. texensis*.
- V. Ray-corollas whitish or pinkish; plants not of Texas or Oklahoma W.
- W. Stems gray-white with a dense pubescence (canescent) 17. *T. incana*.
- W. Stems merely lightly to moderately strigose 19. *T. strigosa*.
- U. Acaulescent, rosulate, long-lived perennials X.
- X. Leaves linear, with dense tufts of long, simple trichomes at the base 8a. *T. mensana* var. *mensana*.
- X. Leaves oblanceolate or spatulate Y.
- Y. Leaves conspicuously thickened 7b. *T. montana* var. *minima*.
- Y. Leaves not conspicuously thickened Z.
- Z. Phyllaries glabrous or the outer ones only lightly pubescent; ray-corollas densely glandular 8b. *T. mensana* var. *Jonesii*.
- Z. Phyllaries conspicuously strigose; ray-corollas glabrous to lightly glandular 17. *T. incana*.

1. *Townsendia formosa* Greene

Townsendia formosa Greene, Leafl. Bot. Obs. & Crit. 1: 213. 1906.
Type: *Metcalfe* 1434, Sawyer's Peak, ca. 9000 ft. alt., Grant Co., New Mexico, 30 Sept. 1904 (CAS, lectotype; COLO, MO, OC, isotypes).

Townsendia pinetorum Greene ex Nels. Coulter. & Nels. Man. Cent. Rocky Mts. 508. 1909 (in synonymy, *nom. nud.*).

Fibrous-rooted perennial, with a basal rhizomatous or stoloniferous mat, producing few to many erect, monocephalous (or very rarely weakly branched), leafy stems; aerial stems striate, lightly strigose, becoming more heavily so near the head with both few- and many-celled, simple trichomes, up to 7 dm. but mostly ca. 3.5 dm. high; basal leaves spatulate or broadly oblanceolate, rounded at the apex and sometimes emarginate, nearly glabrous except for the ciliate margin and sometimes pubescent midrib, 1.5-8 cm. long, 0.5-2 cm. wide; lower cauline leaves similar, becoming more oblanceolate; middle and upper cauline leaves gradually becoming smaller upward, the uppermost often linear or lanceolate and sometimes with a slightly scarious margin; receptacle conical, involucres 1.5-3 cm. wide, 1-1.5 cm. high; phyllaries in 4-6 series, ovate, obovate or oval and the inner becoming lanceolate, apex acute, acuminate or obtuse, broadly scarious-margined and minutely ciliate, nearly glabrous or lightly pubescent along the midrib, 4-14 mm. long, 1.5-5.6 mm. wide; ray-florets ca. 20-35; ray-corollas white on the adaxial surface and blue-purple or mauve abaxially except for the white margins, inconspicuously glandular on the abaxial surface, 14-26 mm. long, 2-3.5 mm. wide; disk-corollas yellow, 3.5-5 mm. long, lightly glandular outside; achenes broadly oblanceolate to broadly obovate, compressed, 2-ribbed, those of the ray sometimes 3-ribbed, glabrous or minutely glandular, 3-4.5 mm. long, 2-2.5 mm. wide; ray-pappus of minute coroniform squamellae, less than 0.5 mm. long; disk-pappus of one to few (mostly 2) short, stiff, plurisetose bristles usually less than 1 mm. long and of short squamellae similar to those of the ray-pappus. $2n = 18$. Reproduction sexual. Mountains of southern New Mexico and adjacent southeastern Arizona. Map 2. Plate XVIII, fig. 1.

Representative specimens. **Arizona.** Apache Co.: Riverside Ranger Station, Greer, Apache Forest, 2700 m. alt., *Eggleston* 17118 (*NY, us); 9 mi. east of McNary on road to Springerville (State Highway 73), White Mountains, *Ferris* 10113 (DS, UC); Thompson Ranch, Black River, White Mountains, *Gooodding* 561 (COLO, GH, NY, *RM, US); Phelps Botanical Area, White Mountains, 9500 ft. alt., *Phillips & Phillips* 3169 (CAS). **New Mexico.** Catron Co.: 0.3 mi. east of Willow Creek Camp Ground, 18 mi. northeast of Mogollon, *Beaman* 994 (*GH); Gilita Camp Ground, 20 mi. northeast of Mogollon, ca. 8000 ft. alt., *Hitchcock et al.* 4403 (CAS, GH, NA, UC, UTC, WS, WTU); Mogollon Mountains, on or near the West Fork of the Gila River, ca. 8500 ft. alt., *Metcalfe* 413 (DS, GH, *MO, NY, POM, RM, UC, US). Grant Co.: Sawyer's Peak, ca. 9000 ft. alt., *Metcalfe* 1434 (CAS, COLO, MO, OC); Black Range, west flank of Sawyer's Peak, Silver Canyon, around Mitchell Gray's cabin, 7300 ft. alt., *Pilsbry* s.n., 20 Aug. 1915 (PH). Otero

Co.: Cludcroft, *Slater s.n.*, Aug. 1914 (us); Sacramento Mountains, *Wooten s.n.*, 23 July 1899 (COLO, DS, OC, POM, *RM, UC, us).

Townsendia formosa is the most sharply defined of the species of *Townsendia*. Its rhizomatous or stoloniferous, fibrous-rooted habit is unique in the genus. None of the taprooted species occupies as mesic a habitat as does this fibrous-rooted species (the evolutionary trend of the genus is toward drier conditions). *Townsendia formosa* is the only species with a conical receptacle. Monocephalous stems are found elsewhere only in *T. Parryi*. The peculiar small pappus also is not duplicated in any other species. All of the foregoing characteristics are interpreted to be primitive features in this genus. These are discussed in greater detail in the sections on generic relationships and trends of evolution.

The primitive characters of *T. formosa* do not obscure the fact that it is related to *T. eximia*. Some degree of similarity can be seen in almost every aspect of the two. Their habits are similar; they have a similar indument; their phyllaries are (slightly) similar; their achenes are very similar; and their pappus is similar. The edaphic requirements and geographical distribution of the two species fit a pattern which, when correlated with the morphological similarities, indicates a close relationship.

2. *Townsendia eximia* A. Gray

Townsendia eximia A. Gray, Mem. Am. Acad. 4 (Pl. Fendl.): 70. 1849. Type: *Fendler* 353, sides of high mountains, Santa Fé Creek, Santa Fé Co., N. Mex., June 28, 1847 (GH, holotype; MO, PH? [not numbered], YU, isotypes).

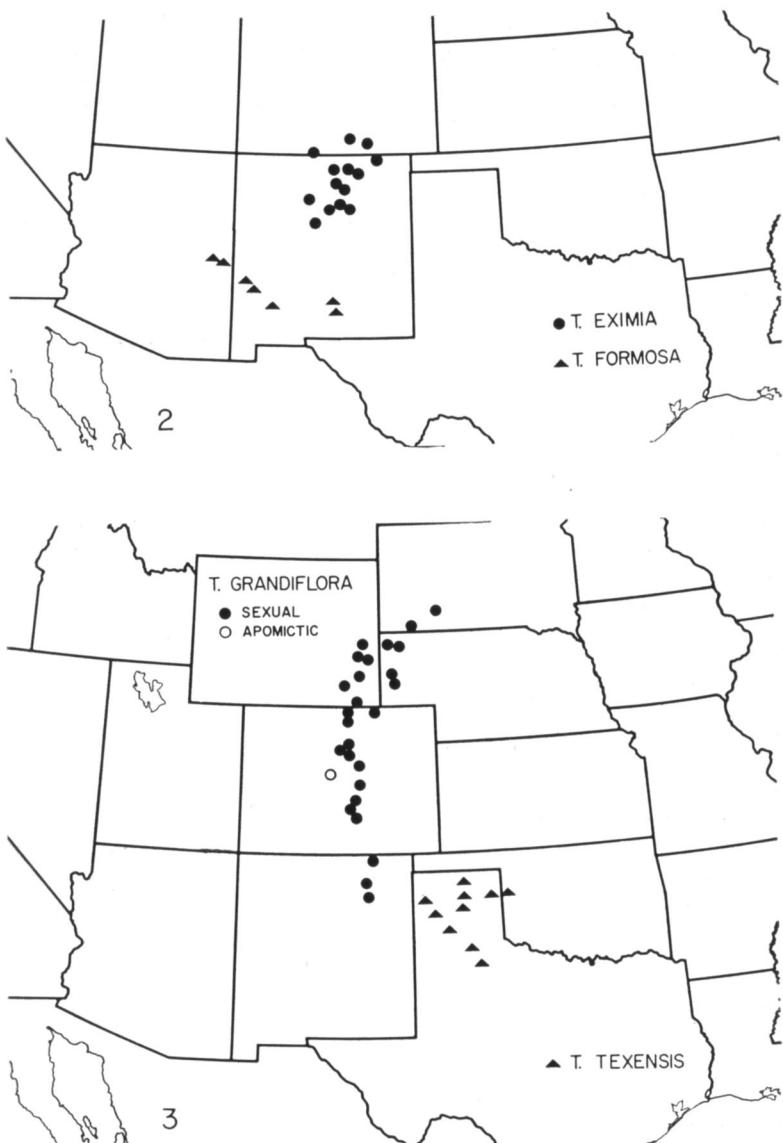
Townsendia Vreelandii Rydb., Bull. Torr. Bot. Club 28: 22. 1901. Type: *Vreeland* 639, side of Veta Mountain, 8500 ft. alt., Huerfano Co., Colo. (NY, holotype; CAN, RM, isotypes).

Caulescent, taprooted, biennial or short-lived perennial, erect or nearly so; stems few to numerous, branching from the base or above or both basally and above, often red-purple, especially near the base, striate, sometimes swollen at junction with the head, lightly to heavily pubescent with pilose-strigose or villous, few-celled trichomes, up to 5 dm. high; basal leaves oblanceolate to slightly spatulate, entire, mucronate, sometimes slightly apiculate, nearly glabrous to lightly strigose especially along the median nerve, 2 lateral nerves frequently present but inconspicuous, up to 13 cm. long and 1.1 cm. wide; upper caudine leaves similar, becoming smaller and more apiculate near the head; involucre 1.2-4 cm. wide; phyllaries in 4-6 series, lanceolate to ovate-lanceolate with bristly-stiff, acuminate apices, glabrous or very lightly strigose, ciliate and scarious-margined, 5-15 mm. long, 1.5-4.2 mm. broad, those of the inner series longest and narrowest; ray-florets ca. 15-55; ray-corollas blue, 8-20 mm. long, 1.5-2.5 mm. wide;

disk-corollas yellow, sometimes red-purple-tinged, 3.5-5 mm. long; achenes obovate to broadly oblanceolate, truncate, compressed, those of the disk-florets 2-ribbed, those of the ray-florets 2-3-ribbed, sparsely pubescent with short, thick, duplex, glochidiate or bifurcate trichomes, slightly denser on the ray than the disk; achenes often papillose, 3.2-4.4 mm. long; pappus of the ray-florets of stiff, coroniform, basally connate squamellae less than 0.5 mm. long; pappus of the disk-florets of similar or slightly longer squamellae, and also of 2, or rarely more, coarse, stiff, plurisetose, barbellate bristles, as much as 4 mm. longer than the squamellae, not equalling the length of the disk-corollas. $2n = 18$. Reproduction sexual. Mountainous areas from south-central Colorado to north-central New Mexico. Map 2. Plate XVIII, fig. 2.

Representative specimens. Colorado. Conejos Co.: Cumbres, *Fertil* s.n., 2 Aug. 1902 (cs). Costilla Co.: east side of La Veta Pass, 9000 ft. alt., *Hitchcock et al.* 4160 (NA, WTU). Huerfano Co.: south side of Mt. Mestas (formerly Veta Mountain), *Beaman* 745 (*GH); 4 mi. northeast of Cucharas Pass, San Isabel National Forest, west of La Veta, 10,000 ft. alt., *Rollins* 1301 (CH, MO, NA, NY); side of Veta Mountain, 8500 ft. alt., *Vreeland* 639 (CAN, NY, RM). Las Animas Co.: Stonewall, 8300-9000 ft. alt., *Beckwith* 233 (*NY); near head of Berwind Canyon on road east of Delagua, 7500 ft. alt., *Robbins* 518 (vc). **New Mexico.** Bernalillo Co.: crest of Sandia Mts., 10,670 ft. alt., *Beaman* 699 (*GH); hillsides, Balsam Park, Sandia Mts., 8200 ft. alt., *Ellis* 56 (*MO, NY, US); Albuquerque, Sandia Mts., *Jones* 4157 (CAS, F, CH, MSC, NY, OC, PH, POM, *RM, US, UTC). Colfax Co.: Cimarron, *Berg* 3135 (cs); Colfax Co. (?): Cimarron Pass in Raton Mts., *McKelvey* 2419 (CH, POM); vicinity of Ute Park, 2200-2900 m. alt., *Standley* 14490 (*NY, US). Mora Co.: 10 mi. northwest of Mora, *Beaman* 719 (*GH). Sandoval Co.: 11 mi. northeast of Jemez Pueblo on U. S. Forest Service road, *Beaman* 704 (*GH); University Field School area, Jemez Springs, *Nelson* 11640 (DS, CH, *MO, MONTU, NY, RM, UC, UTC); Sandia Mts., *Wooton* s.n., 4 Aug. 1910 (us). San Miguel Co.: vicinity of Las Vegas, *Anect* 41 (CAS, GH, US); hillside along Pecos River, *Drouet & Richards* 3316 (DS, CH, MICH, *MO). Santa Fé Co.: $\frac{1}{2}$ mi. west of Glorieta in Glorieta Pass, *Beaman* 717 (*GH); sides of high mountains, Santa Fé Creek, *Fendler* 353 (CH, MO, PH? [not numbered], YU); Cañoncito, 7200 ft. alt., *Heller & Heller* 3726 (DAO, DS, GH, ILL, *MO, MSC, ND, NY, OC, POM, RM, RSA, US, WS, WTU); canyon wall 20 mi. south of Golden, ca. 7000 ft. alt., *Hitchcock et al.* 4229 (DS, NA, UC, WTU). Taos Co.: 18 mi. south of Taos, *Beaman* 723 (*GH); 9 mi. east of Questa, *Beaman* 740, (*GH); 5 mi. south of Questa, ca. 7000 ft. alt., *Hitchcock et al.* 4175 (CAS, DS, CH, NA, UC, WTU).

Plants of the southernmost geographical segment of this species have only slightly bristly-acuminate phyllaries that have a very sharp demarcation between the ciliate margin and herbageous inner portion. The rest of the species is characterized by strongly bristly-acuminate phyllaries with a transitional scarious



MAPS 2-3. 2. Geographic distribution of *Townsendia formosa* and *T. eximia*. 3. Geographic distribution of *Townsendia texensis* and sexual and apomictic *T. grandiflora*.

area between the ciliate margin and herbaceous inner portion. The southern populations of *T. eximia* tend to approach their more southern neighbor, *T. formosa*, but there is no evidence which suggests hybridization between the two. Possibly this resemblance is merely an indication of relatedness of the two species. Further evidence of their relationship was outlined in the discussion of *T. formosa*.

Under most conditions *T. eximia* is a biennial, but in high-elevation populations, such as those near the crest of the Sandia Mountains and in the Raton Mountains, the perennial habit is well-developed. It appears that life-duration is not a strongly-fixed genetic character in the species. A parallel variation occurs in *T. scapigera* in eastern California where it occupies low- and high-elevation habitats. Likewise, several other members of the genus may be biennial or perennial, depending upon the habitat which they occupy.

In the southern portion of its range *T. eximia* is usually an erect, sparsely-branched plant; to the north, especially in southern Colorado, it is suberect and more abundantly branched. In this feature *T. eximia* approaches *T. grandiflora*. Two collections, Standley 13289 and Standley 6357, from the vicinity of Raton, New Mexico, strongly suggest hybridization between these species. The plants in question have the widely branched habit of *T. grandiflora*. The disk-pappus, of several bristles, is intermediate between the two. The very bristly-acuminate phyllaries are suggestive of *T. grandiflora*. Most of the other characters are typical of *T. eximia*, and these plants have been referred to that species. Field studies might reveal the relative importance of whatever gene interchange occurs between *T. eximia* and *T. grandiflora*.

3. *Townsendia grandiflora* Nutt.

Townsendia grandiflora Nutt. Trans. Am. Phil. Soc. VII: 306. 1840.
Type: Nuttall s.n., "On the Black Hills, (or eastern chain of the Rocky Mountains,) near the banks of the Platte," 1834 (BM, holotype, examined by Dr. R. C. Rollins; GH!, PH!, isotypes).

Caulescent, taprooted biennial; root-stem junction enlarged; stems branched at the base, few to numerous, less branched above, mostly spreading and suberect, striate-angled, with a moderate to dense strigose-pilose pubescence, ca. 1.5-30 cm. long; basal leaves spatulate, entire, obtuse, sometimes slightly mucronate, lightly strigose above, nearly glabrous below, up to 5 cm. long and 1 cm. wide, mostly deciduous by flowering time; cauline leaves spatulate to oblanceolate, entire, acute or slightly acuminate or obtuse, mucronate, with a fairly conspicuous median nerve, lightly strigose especial-

ly along the nerve and margins, up to 9 cm. long (averaging ca. 4 cm.) and 1 cm. wide (averaging ca. 4 mm.); heads borne at the ends of the stems, often subtended by one or a few leaves; involucres 15-30 mm. wide, 10-18 mm. high; phyllaries in 4-7 series, ovate-lanceolate or lanceolate with bristly-acuminate apices, ciliate and broadly scarious-margined, with a median green or rarely greenish-purple streak, glabrous or lightly strigose on the outer surface, 4-13 mm. long, 1.5-4.5 mm. wide, the next-to-inner series usually longest; ray-florets ca. 20-40; ray-corollas white above and usually with a median pink or purplish stripe below, 12-23 mm. long, 1-2.5 mm. wide; disk-corollas yellow, rarely pink-purplish tipped, 4-6 mm. long; achenes oblanceolate, compressed, 2-ribbed, lightly to densely pubescent (denser on the disk than the ray) with rather short, thick, duplex, glochidiate or bifurcate hairs, 3.0-4.5 mm. long, 1.1-1.8 mm. wide; ray-pappus of short, coroniform squamellae or plurisetose bristles, not more than 2 mm. long; disk-pappus of ca. 15-30 stiff, plurisetose, barbellate bristles, 3.8-6 mm. long. $2n = 18$ in sexual plants, and $2n = 27-36$? in apomictic plants (the latter inferred from pollen measurements). Reproduction mostly sexual, rarely apomictic. Southwestern South Dakota south to northeastern New Mexico. Map 3. Plate XVIII, fig. 3.

Representative specimens. Colorado. Boulder Co.: southeast-facing slope near summit of Flagstaff Mtn., *Beaman & Preece* 509 (*ws); El-dorado Springs, 5300 ft. alt., *Clokey* 2810 (CAN, CAS, DS, F, *NY, RM, UC, US). Custer Co.: southern slope, Hardscrabble Creek, above Wet-more, 6000 ft. alt., *Klinger* s.n., 1 Sept. 1951 (*cs). Douglas Co.: hill-side 10 mi. north of Castle Rock, 6000 ft. alt., *Ownbey* 684 (*RM, ws). El Paso Co.: mountain side, Manitou, *Shear* 3687 (NY, *US). Fremont Co.: 11 mi. east of Canon City, *Waterfall* 11490 (*UC). Jefferson Co.: Mount Morrison, southwest of Denver, 6100 ft. alt., *Constance & Rollins* 1932 (NA, UC, *ws). Gilpin Co.: Central City, *Scovell* s.n., 1869 (*MICH). Larimer Co.: hill 2 mi. west of Bellvue, *Preece & Turner* 2858 (*ws); Owl Canyon, ca. 18 mi. northwest of Fort Collins, *Weber* 4873 (*COLO). Park Co.: 7 mi. south of Fairplay, 9000 ft. alt., *Ripley & Barneby* 10371 (†CAS). Pueblo Co.: 2½ mi. northwest of Rye, *Beaman* 744 (*CH). Weld Co.: Grover, *Johnston* 228 (*RM). **Nebraska.** Banner Co.: hills south of Pumpkin Seed Valley, *Rydberg* 160 (*NY, US). Dawes Co.: Bryan Canyon, Crawford, *Hapeman* s.n., June 1939 (*MO, NY, UC). Sioux Co.: hilltop 5 mi. east of Harrison, 5100 ft. alt., *Ripley & Barneby* 9106 (*CAS). Scotts Bluff Co.: Scotts Bluff, 5000 ft. alt., *Hapeman* s.n., 13 July 1935 (MO, *UC). **New Mexico.** Colfax Co.: Raton Mountains, *Bell* s.n., Aug. 1867 (*PH); Goat Mountain, Raton, *Cockerell & Cockerell* s.n., 26 Aug. 1900 (US). Mora or Colfax Co.: prairie between Ocate Creek and Rio Colorado, *Fendler* 533 (*MO); Mora River prairie, *Fendler* 157 (*MO). **South Dakota.** Shannon Co.: Cedar Draw, 8 mi. northeast of Rocky Ford, *McIntosh* s.n., (*DAO); sandbars, White River, *Over* 2399 (US). Washabaugh Co.: summit of Snake Butte, *Over* 2069 (*US). **Wyoming.** Albany Co.: South Sibylee, *Nelson* 7373 (CM, COLO, *GH, ILL, MO, NY, POM, RM, US). Goshen Co.: Fort Laramie, *Nelson* 8312 (*GH, MO, RM, US). Lar-

amie Co.: Cheyenne, 1850 m. alt., *Eggleston* 12563 (*us). Niobrara Co.: Mexican Mines (Spanish Diggings), *Nelson* 578 (GH, ILL, MSC, ND, *PH, RM, WS). Platte Co.: hillsides 6 mi. north of Chugwater, *Porter* 3391 (DS, GH, *MO, NY, RM, UC, US, WTU); slopes on the Oregon Trail near Warm Springs, 3 mi. west of Guernsey, 4400 ft. alt., *Porter* 4910 (COLO, DAO, *GH, MONT, OKL, PH, RM, RSA, UC, US, UTC, WTU).

The bristly-acuminate phyllaries, erect or suberect, biennial habit, allopatric ranges, and same flowering times suggest a close relationship between *T. grandiflora* and *T. eximia*. *Townsendia grandiflora* is adapted to the relatively arid foothills east of the Front Range in Colorado while *T. eximia* occupies slightly more moist habitats at higher elevations in mountains to the south. A *T. eximia* stock may have migrated north along the foothills area and become isolated from the central concentration of *T. eximia*. During that isolation the two species as they are now known probably developed. *Townsendia grandiflora* is the more specialized of the two.

An interesting parallel in the occurrence of apomixis in *T. grandiflora* and in another biennial, *T. scapigera*, has been mentioned in the discussion of the latter species. Unlike apomictic *T. scapigera*, the apomicts of *T. grandiflora* appear to have retained the biennial nature of their sexual precursors (the apomicts of *T. scapigera* are short-lived perennials, although most plants of the species are biennial). It should be noted that the locality of *Ripley & Barneby* 10371 is the highest-elevation station now known for this species, and is the only station from which the species is known to be apomictic.

4. *Townsendia texensis* Larsen

Townsendia texensis Larsen, Ann. Mo. Bot. Gard. 14: 15, pl. 3. 1927. Type: Eggert s.n., rocky bluffs of the Red River, Randall Co. (?), Texas, 13 Aug. 1900 (MO 121021, holotype, missing; GH!, POM!, isotypes).

Caulescent, taprooted biennial; root-stem junction enlarged or elongated; stems branched mostly at the base, few-branched above, the central stem erect and the laterals spreading-suberect, striate, with a moderate to dense strigose-pilose pubescence, ca. 0.5-2.5 cm. long; basal leaves mostly deciduous by flowering time; cauline leaves oblanceolate, acute, mucronate, 1-nerved, lightly strigose on both surfaces to nearly glabrous, up to 60 mm. long and 5 mm. wide; heads borne at the ends of the stems, often subtended and surpassed by a few leaves; involucres 1.3-2 cm. wide, 0.7-1.1 cm. high; phyllaries in 4-6 series, ovate-lanceolate or lanceolate, acute or slightly acuminate, ciliate and broadly scarious-margined, with a darker median streak, strigose on the outer surface or sometimes nearly glabrous, 3.5-10 mm. long, 0.5-2.4 mm. wide, the inner series usually longest; ray-florets ca. 25-40;

ray-corollas blue or very rarely white, sometimes pubescent on the abaxial surface, 0.9-1.8 cm. long, 1.5-2.5 mm. wide; disk-corollas yellow, 3.5-5 mm. long; achenes oblanceolate, compressed, 2-ribbed, lightly to moderately pubescent with rather short, thick, duplex, glochidiate hairs, 3-3.8 mm. long, 1.1-1.7 mm. wide; ray-pappus of coroniform-concreted squamellae or short, plurisetose bristles, usually not more than 1 mm. long but rarely up to 2.5 mm. long; disk-pappus of ca. 16-25 plurisetose, barbellate bristles, equaling or shorter than the disk-corollas. $2n = 18$. Reproduction sexual. Texas Panhandle and adjacent western Oklahoma. Map 3. Plate XVIII, fig. 4.

Representative specimens. **Oklahoma.** Roger Mills Co.: side of one of the Antelope Hills, in northwestern part of county, *Beaman* 691 (GH); Antelope Hills, *Goodman* 2614 (GH, MO, NY, OKL, RM, WTU). **Texas.** Briscoe Co.: 5.6 mi. northwest of Quitaque, *Cory* 17306 (NA). Carson Co.: ca. 4 mi. south of Borger, *Beaman* 696 (GH). Hansford Co.: near Paloduro Creek, 6 mi. southeast of Gruver, *Beaman* 694 (*GH); 5 mi. southeast of Gruver, *Shinners* 8227 (*RM, UC). Hartley Co.: 13.6 mi. west of Channing, *Cory* 16458 (NA). Hemphill Co.: near the Canadian River, 5 mi. south of Canadian, *Beaman* 693 (GH). Hutchinson Co.: 10 mi. southeast of Stinnett, *Cory* 16352 (NA). Motley Co.: hillside 3 mi. west of Matador, *Waterfall* 7839 (GH, *MO). Oldham Co.: 4 mi. north and 1½ mi. east of Vega, 4000 ft. alt., *Howard* 159 (NA). Randall Co.: bluffs, 1 mi. north of Canyon, *Beaman* 698 (GH).

In most of its morphological characters, *T. texensis* is intermediate between *T. eximia* and *T. grandiflora*. It is closely related to but distinct from both. *Townsендia texensis* and *T. grandiflora* probably are about equally derived species from a *T. eximia* ancestral stock. The non-cuspidate (rarely minutely cuspidate) phyllaries distinguish *T. texensis* from the other two species.

My field observations of *T. texensis* in Roger Mills County, Oklahoma and several counties in the Texas Panhandle indicate that it is abundant in that area. It grows on Cretaceous limestones exposed by stream erosion of the deep, black soils of the high plains.

5. *Townsендia glabella* A. Gray

Townsендia glabella A. Gray, Proc. Am. Acad. 16: 86. 1880. Type: *Newberry* s.n., La Pagosa (Pagosa Springs), Archuleta Co., Colo., July 29, 1859 (GH, holotype; NY, YU, isotypes).

Townsендia Bakeri Greene, Pittonia 4: 157. 1900. Type: *Baker* 727, Los Pinos (Bayfield), La Plata Co., Colo. (ND, lectotype; F, GH, *MO, NY, POM, RM, UC, US, isotypes).

Long-lived, decumbent-cespitoso, taprooted perennial; caudex widely branched, becoming woody and subterranean; young stems at ends of the

caudex branches leafy, more densely so near the tips, up to 5.5 cm. long, often with one or a few peduncles in the axils of the upper leaves; leaves spatulate to oblanceolate, entire, the apex sometimes apiculate and mucronate or sometimes rounded, blades dark green, shiny, glabrous or nearly so below, very lightly strigose above, up to 65 (averaging 45) mm. long, 4-11 mm. wide; peduncles up to 7 cm. long, sometimes expanded at junction with the head, naked or rarely with a small bract near the head, striate, with light pilose-strigose pubescence becoming denser near the head, involucres 8-24 mm. wide, 7.8-12.3 mm. high, often broadly expanded at maturity; phyllaries in 3-6, mostly 4, series, broadly lanceolate or oblanceolate, acute or rarely slightly acuminate, glabrous or nearly so, scarious-margined, ciliate, 3.5-10 mm. long, 1.2-2.5 mm. wide, the inner longest; ray-florets ca. 12-35; ray-corollas white to light blue-pink (lavender-purple), glabrous, 8-14 mm. long, 1.5-2.5 mm. wide; disk-corollas yellow, sometimes greenish or pinkish purple-tipped, 3.6-5.3 mm. long; achenes oblanceolate, compressed, 2-ribbed, those of the ray-florets rarely 3-ribbed, sparsely pubescent with long, slender, duplex, glochidiate hairs; ray-achenes usually minutely papillose, disk-achenes smooth; ray-pappus of short, plurisetose, barbellate bristles, rarely exceeding 1.8 mm. in length; disk-pappus of ca. 15-35 plurisetose, barbellate bristles, 4-7 mm. long, mostly exceeding the length of the disk-corollas, rarely of the same length or shorter. $2n = 18$. Reproduction sexual. Southwestern Colorado. Map 5. Plate XIX, fig. 1.

Representative specimens. **Colorado.** Archuleta Co.: 9 mi. southeast of Pagosa Springs, Beaman 761 (*GH); hills, Pagosa Springs, 2160 m. alt., Bethel, Willey & Clokey 4340 (CAN, CAS, COLO, DS, F, MICH, *MO, MONTU, NY, PH, POM, RM, UC, US, UTC, WS, WTU); 1.5 mi. southeast of Pagosa Springs, Turner 2892 (ws); mesa slopes ca. 12 mi. north of Arboles, 6400 ft. alt., Weber & Livingston 6238 (COLO, DAO, *RM, RSA, WS, WTU). La Plata Co.: hillside near Dix, 8500 ft. alt., Baker, Earle & Tracy 548 (CM, F, GH, MICH, *MO, NY, OC, POM, RM, UC, US); 7.5 mi. east of the Montezuma Co. line, east of Mancos, Beaman 772 (*GH); 15 mi. west of Durango, Waterfall 11716 (*UC). Montezuma Co.: Mesa Verde National Park, Nelson 10419 (GH, *MO, MONTU, NY, RM, UC).

This species is closely related to *T. eximia*. Such features as the similar involucral bracts, similar vesture, and similar habit (of the high-elevation types of *T. eximia* and *T. glabella*) suggest the relationship. *Townsendia glabella* has the more specialized form of the two, and appears also to have much more specialized habitat requirements. It is abundant only on the Mancos shales of southwestern Colorado. Its endemism may be an expression of precise edaphic and climatic requirements that are satisfied only in that area.

Even though its range is restricted, *T. glabella* is somewhat variable. Phyllary variation is especially noticeable. For example, in Baker 727 some plants have slightly bristly-acuminate phyllaries; others have acute, and in one plant (POM) broadly obtuse,

phyllaries. The plants of this collection also have shorter peduncles than do plants of the other collections. It is perhaps the minor divergence of *Baker* 727 from typical *T. glabella* which led Greene to describe *T. Bakeri*.

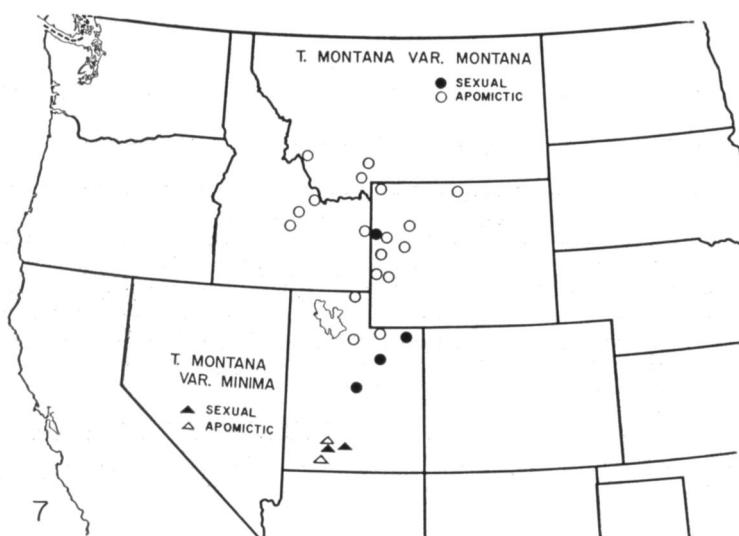
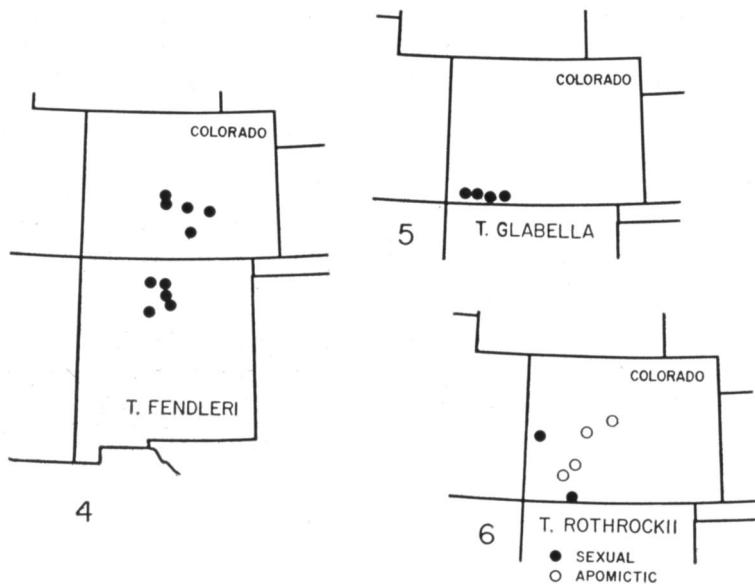
One of the plants which Gray had at hand when he described *T. glabella* is a teratological form. Its ray-corollas, with long tubes and two conspicuous lateral lobes, are intermediate between ray- and disk-corollas. The ray-pappus is half as long as the disk-pappus. I have not considered the abnormal features of this particular plant in the key.

6. *Townsendia Rothrockii* A. Gray ex Rothrock

Townsendia Rothrockii A. Gray ex Rothrock, Wheeler Rept. U. S. Geograph. Surv. 6 (Bot.): 148. Pl. VII, A. 1878. Type: *Rothrock* 875, South Park, Park Co., Colorado, 13,500 ft. alt., July 1873 (f, holotype; GH, †NY, isotypes).

Rosulate perennial with taproot; caudex short-branched, with tufts of leaves at the ends, becoming woody, often subterranean; leaves spatulate-ob lanceolate, entire, acute or obtuse, sometimes mucronulate, conspicuously thickened, shiny, glabrous or very lightly strigose, 10-35 mm. long and 2-7 mm. wide; heads sometimes nearly sessile, but usually on short peduncles up to 2.7 cm. long; peduncles naked or with a phyllary-like bract near the involucre, striate, villous; involucres 12-28 mm. wide, 8-12 mm. high; phyllaries in 4-6 series, elliptical, ovate, obovate, broadly lanceolate, or oblanceolate, acute, sometimes rounded at the tip, glabrous, scarious-margined, ciliate, red-tinged near the apex, 6-9.5 mm. long, 2-4 mm. wide; ray-florets ca. 18-40; ray-corollas blue, glabrous, 8-16 mm. long, 2-3 mm. wide; disk-corollas yellow, often slightly greenish tipped, 3.3-4.8 mm. long; achenes broadly oblanceolate, compressed, 2-ribbed, those of the ray-florets rarely 3-ribbed; ray-achenes moderately pubescent with long, thin, duplex, glochidiate hairs, papillose; disk-achenes lightly pubescent with hairs similar to those of the ray, or nearly glabrous, not papillose; ray-pappus much reduced, of plurisetose, coroniform squamellae or bristles not over 1.5 mm. long; disk-pappus of ca. 15-30 plurisetose, barbellate bristles, 3.2-6 mm. long, usually about equal to or slightly exceeding the length of the disk corollas. $2n = 18?$ in sexual plants (inferred from pollen measurements) and $2n = 36$ in apomictic plants. Mountains of southwestern Colorado. Map 6. Plate XIX, fig. 2.

Representative specimens. Colorado. Archuleta Co. (?): mts. east of Bayfield, 10,000 ft. alt., *Bequaert* s.n., July 1929 (*GH). Gunnison Co.: crest of ridge between Avery Mtn. and Virginia Mtn., near Gothic, *Beaman & Barclay* 798 (†GH); Taylor Pass, 12,400 ft. alt., *Langenheim* 442 (†COLO); foot of Matchless Mtn., 11,000 ft. alt., *Langenheim* 1310 (†COLO). Hinsdale Co.: Crystal Lake near Lake City, 11,000 ft. alt., *Pease* s.n., 28 June 1878 (†YU). Mesa Co.: 6 mi. above Taylor Ranch, between Gateway and Whitewater, 8000 ft. alt., *Kelly* 1643 (*COLO). Park Co.: Hoosier Ridge, *Beaman, Weber & Preece* 516 (†WS); Hoo-



MAPS 4-7. 4. Geographic distribution of *Townsendia Fendleri*. 5. Geographic distribution of *T. glabella*. 6. Geographic distribution of sexual and apomictic *T. Rothrockii*. 7. Geographic distribution of sexual and apomictic *T. montana* var. *montana* and *T. montana* var. *minima*.

sier Ridge, 12,000-13,000 ft. alt., *Weber & Rollins* 7166 (CAS, COLO, DAO, CH, fRM, RSA, WS, WTR); South Park, *Wolf* 417 (NY, US). San Juan Co.: Engineer's Peak, 12,000 ft. alt., *Purpus* s.n., 27 July 1893 (F, fCH, MICH, MSC).

Townsendia Rothrockii appears specialized for existence in a very cold climate. Its morphological specialization obscures its relationship with other species, but possibly its nearest, although not too close, relationship may be with *T. glabella*.

In Park and Gunnison Counties, Colorado, two apomictic populations of the species have very unusual habitats. At elevations over 12,000 ft. they grow in red sandstone fragments under snowbanks, flowering as the snow melts away. Such peculiar conditions perhaps are not required by the species but may be optimum, thus helping to explain the narrow endemism of *T. Rothrockii*.

7. *Townsendia montana* M. E. Jones

Rosulate-pulvinate, taprooted perennial; caudex becoming much-branched, often partly subterranean, the old leaf-bases often persisting for several years, sometimes becoming much elongate in plants growing in talus, bearing the persistent scars of old leaves and developing adventitious roots; leaves spatulate, sometimes thickish, entire, obtuse, sometimes mucronate, rarely emarginate, nearly glabrous to moderately strigose, up to 40 mm. long and 8 mm. wide; heads pedunculate (rarely sessile); peduncles naked or nearly so, swollen at junction with the head, with pilose-strigose pubescence, up to ca. 6.5 cm. long; involucres obconical at base, 8-15 mm. wide, 6-12 mm. high; phyllaries in 3-6, mostly 4, series, oblong, obovate, oblanceolate to lanceolate, obtuse and rounded at the apex or rarely acute, red-scarious-margined, ciliate, glabrous or very lightly strigose on the abaxial surface, 2-8 mm. long, 0.8-2.9 mm. wide, the inner longest; ray-florets ca. 12-30; ray-corollas blue, white, or pink, sometimes glandular on the abaxial surface, 6-12 mm. long, 1-3.5 wide; disk-corollas yellow, sometimes pink-greenish tipped, 3.3-5.2 mm. long; achenes narrowly or broadly oblanceolate, compressed, 2-ribbed, those of the ray-florets sometimes 3-ribbed, glabrous or sparsely pubescent with rather long, duplex, bifurcate hairs, or with delicate, tangled, duplex, bifurcate or glochidiate hairs, sometimes papillose, 3.7-5.2 mm. long, 1.0-1.6 mm. wide; pappus of the ray- and disk-florets similar, of ca. 15-35 plurisetose, barbellate bristles (rarely pappus of the ray-florets very short). Reproduction sexual and apomictic. Western Montana and Wyoming to central Idaho and south to southern Utah.

KEY TO THE VARIETIES

- Heads at least slightly pedunculate; rays blue or white; leaves not involute, not conspicuously thickened..... 7a. var. *montana*.
Heads sessile; rays pink; leaves involute, conspicuously thickened..... 7b. var. *minima*.

7a. *Townsendia montana* M. E. Jones var. *montana*

Townsendia montana M. E. Jones, *Zoe* 4: 262. 1893. Type: *Jones s.n.*, above the Flagstaff Mine, Alta, 9500 ft. alt., Salt Lake Co., Utah, 7 August 1879 (POM 40755, holotype).

Townsendia alpigena Piper, *Bull. Torr. Bot. Club* 27: 394. 1900. Type: *Cusick* 2294, subalpine ridges of the Wallowa Mts., 7000 ft. alt., Wallowa Co., Oregon, July 31, 1899 (\dagger ws, lectotype; F, GH, MO, MSC, UC, US, isotypes).

Townsendia dejacta A. Nels. *Bot. Gaz.* 37: 267. 1904. Type: *Goodding* 1238, Dyer Mine, Uinta Mts., ca. 3000 m. alt., Uintah Co., Utah, July 3, 1902 (*?RM, holotype; MO, US, isotypes).

$2n = 18$ in sexual plants and $2n = 36$ in apomictic plants. Reproduction predominantly apomictic. Mountains of western Montana to eastern Oregon and south to central Utah. Map 7. Plate XIX, fig. 3.

Representative specimens. **Idaho.** Blaine Co.: Mt. Hyndman, Sawtooth Range, 8000 ft. alt., *Thompson* 13626 (CH; MO p.p., with 1 plant of *T. leptotes*; NY, PH, US, \dagger ws, WTU). Custer Co.: southeast of Double Springs summit, 8 mi. northeast of Dickey, 8500 ft. alt., *Cronquist* 3197 (CH, \dagger DS, MO, all p.p., with plants of *T. leptotes*); head of Mahogany Creek northwest of Borah, *Hitchcock & Muhlick* 11039 (\dagger NY, WTU). Fremont Co.: east side of Mt. Jefferson, southwest of Henry's Lake, 9500 ft. alt., *Cronquist* 1924 (DS, \dagger MO, UTC, WTU); mountains northeast of Henry Lake, 8700 ft. alt., *Payson & Payson* 1986 (CAS, \dagger CM, CH, MO, NY, RM, UC). Lemhi Co.: Liberty Range, west of Gilmore, *Christ & Ward* 14886 (\dagger NY p.p., with 5 plants of *T. leptotes*). Teton Co.: Teton Peaks, *Davis s.n.*, July 1930 (\dagger DS). **Montana.** Beaverhead Co.: ridge connecting Sheep and Black Lion Mts., Pioneer Range, ca. 9300 ft. alt., *Hitchcock & Muhlick* 13003 (DS, \dagger MO, RM, RSA, UC, WS, WTU). Gallatin Co.: without definite locality, 8500 ft. alt., *Tweedy s.n.*, Aug. 1886 (\dagger XU). Madison Co.: $\frac{1}{2}$ mi. north of Kock Peak, Taylor Mts., *Hitchcock & Muhlick* 15176 (\dagger NY, WTU); head of Cottonwood Creek, Tobacco Root Range, 9000 ft. alt., *Blankinship s.n.*, 10 Aug. 1902 (\dagger MONT, UTC, WTU). **Oregon.** Wallowa Co.: subalpine ridges of the Wallowa Mts., 7000 ft. alt., *Cusick* 2294 (F, GH, MO, MSC, UC, US, \dagger ws); source of Imnaha River, 2700 m. alt., *Cusick* 3702 (ws, WTU); summit, east side of Lostine Canyon, 18 mi. above Lostine, *Peck* 17866 (DS, \dagger NY); slope above Ice Lake, 3000 m. alt., *Peck* 18546 (DS, NY). **Utah.** Cache Co.: trailside, saddle of Mt. Naomi, 9500 ft. alt., *Maguire, Hobson, & Maguire* 14227 (CAN, \dagger UTC, WTU). Duchesne Co.: 14 mi. south of Theodore, 7000 ft. alt., *Jones s.n.*, 18 May 1908 (*?POM). Salt Lake Co.: crest of ridge above Flagstaff Mine at Alta, *Beaman* 843 (\dagger CH); headwaters of Little Cottonwood Creek, above Alta, *Rydberg* 6607 (CAN, \dagger NY, RM, US). San Pete Co.: side of Mt. Baldy, 2 mi. west of intersection of skyline drive and road from Mayfield, *Beaman* 806 (*CH); ridges and slopes, Mayfield Canyon, $\frac{1}{2}$ mi. above Ranger Station, 10,982 ft. alt., *Maguire* 19987 (*NY, US, UTC). Summit Co.: ridge

east of East Fork of Bear River, Uinta Mts., 11,000 ft. alt., *Goodman & Payson* 452 (OKL, †RM); divide between East Fork of Bear River and Black's Fork, 10,500 ft. alt., *Goodman & Hitchcock* 1517 (F; GH p.p., with 4 plants of *T. leptotes*; †NY p.p., with 3 plants of *T. leptotes*). Uintah Co.: Dyer Mine, Uinta Mts., *Goodding* 1238 (MO, *? RM, US); rocky crest of east side of Whiterocks Canyon between Red Pine and Paradise Creeks, 10,000 ft. alt., *Graham* 10065 (*CM, *NA). Wyoming. Big Horn or Sheridan Co.: summit of Big Horn Mts., *Blankinship s.n.*, 1890 (†NY). Fremont Co.: Indian Point, 8 mi. northeast of the Dennison Ranch above Wiggins Fork, 10,000 ft. alt., *Porter* 6625 (†UC). Lincoln Co.: ridge near Cottonwood Lake, east of Smoot, 10,400 ft. alt., *Payson & Armstrong* 3706 (CH, †MO, MSC, RM); Dead Man Peak, 9500 ft. alt., *Williams* 1301 (CAS, †MO, RM, UTC). Sublette Co.: summit, Piney Mtn., 25 mi. west of Big Piney, *Payson & Payson* 2694 (CH, †MO, POM, RM, UC, US); slopes in the vicinity of Green River Lakes, 10,300 ft. alt., *Payson & Payson* 4542 (CH, †MO, MSC, PH, RM, ws); slopes in the vicinity of Green River Lakes, 10,300 ft. alt., *Payson & Payson* 4549 (†RM). Teton Co.: southeast facing slope on south side of Teton Pass, ca. 9000 ft. alt., *Beaman & Preece* 505 (*ws); Teton Pass Mts., east of Victor, Idaho, 9200 ft. alt., *Payson & Payson* 2078 (CAS, CM, GH, MO, *NY, RM); Teton Pass, 9000 ft. alt., *Ripley & Barneby* 8898 (*CAS); Sheep Mtn., alpine, 10,200 ft. alt., *Tweedy* 532 (†NY, †YU); vicinity of Teton Pass, 9500 ft. alt., *Williams* 786 (*CAS, CH, MO, NY, RM, UTC). Yellowstone National Park: Mammoth Hot Springs, *Oleson* 116 (†RM).

7b. *Townsendia montana* M. E. Jones var. *minima* (Eastwood) Beaman, comb. nov.

Townsendia minima Eastwood, Leafl. West. Bot. 1: 206. 1936.
Type: *Eastwood & Howell* 727, Bryce Canyon, Garfield Co., Utah, June 19, 1933 (CAS, holotype).

$2n = 18$? in sexual plants (inferred from pollen measurements) and $2n = 27$ in apomictic plants. Southwestern Utah. Map 7. Plate XIX, fig. 4.

Representative specimens. Utah. Garfield Co.: Red Canyon near Bryce, 7000 ft. alt., *Cottam* 9691 (†UT); Red Canyon, *Eastwood* 785 (CAS); Red Canyon, 10 mi. from Bryce Park entrance, *Hitchcock* 2962 (*WTU); Red Canyon, 10 mi. west from Bryce Canyon, 7500 ft. alt., *Harrison* 9016, (*NA); head of canyon above Tropic, 7000 ft. alt., *Jones* 5312ar (NY, POM, US); Bryce Canyon, *Maguire* 5034 (CAN, *UTC, WRTU); Pink Cliffs, 1 mi. east of Pine Lake, Table Cliff Plateau, Powell National Forest, 9000 ft. alt., *Maguire* 19120 (CH, NY, UTC). Kane Co.: near summit of Pink Cliffs, headwaters, left fork Virgin River, 15 mi. northwest of Orderville, *Maguire* 18807 (UTC); 5 mi. west of Long Valley Junction on Highways 14 and 89, *Preece & Turner* 2462 (†CH, †ws).

Townsendia montana appears to be a continuation of the *T. eximia*-*T. glabella* evolutionary line. Its relationship with this

group is indicated by the glabrate leaves, lightly pubescent or glabrous achenes, and broad, glabrate phyllaries. *Townsendia montana* may be the evolutionary result of isolation of this (*T. eximia-T. glabella*) stock in the mountains of Utah away from the central core of the genus in the Rocky Mountains.

Variety *montana* is mostly a high-elevation type, occurring at about timberline. Variety *minima* is found at somewhat lower elevations, but probably does not occur below the ponderosa pine belt. It has been collected at elevations as high as 9000 ft.

Although var. *montana* is known from very few collections that represent sexually reproducing populations, each of these is slightly different morphologically from the others. At the southern extremity of its range, the San Pete County population is a fairly close morphological approach to var. *minima*.

The most problematical portion of *T. montana* is in the Uinta Mountains. A collection (*Goodding 1238*) described by Nelson as *T. dejuncta* is somewhat distinct from the other collections of *T. montana* var. *montana*. Variety *montana* usually has pedunculate heads, while the heads of this collection are sessile. Typical var. *montana* has glabrate, spatulate leaves, and this material has moderately pubescent, oblanceolate leaves. In these unusual features *Goodding 1238* seems to approach *T. leptotes*. Another collection (*Graham 10065*) from the same area represents the only known population of *T. montana* with a short ray-pappus. It seems significant that *T. leptotes* in this area also has a short ray-pappus. Only apomictic *T. leptotes* is now known in the Uinta Mountains, but sexual material could be there now or recently may have been there. Sexual *T. leptotes* of the long ray-pappus form is nearby in western Moffatt County, Colorado (*Wolf & Dever 5193*). The type of variation in the collections *Goodding 1238* and *Graham 10065* seems most readily explainable on the basis that hybridization between *T. montana* var. *montana* and *T. leptotes* has occurred. It should be noted also in this connection that the collection *Goodman & Hitchcock 1517*, from the Uinta Mountains, is a mixture of *T. montana* var. *montana* and *T. leptotes*. These specimens of the two species are very difficult to distinguish from each other and appear to be from apomictic populations of hybrid derivation.

The sexual population of *T. montana* var. *montana* in Wyoming at Teton Pass, Teton County, is of interest because of its considerable intra-population variation. Four collections, *Beaman & Preece 505*, *Payson & Payson 2078*, *Ripley & Barneby 8898*, and *Williams 786*, each consisting of a fairly large number of plants,

have been made at or near the same spot. Plant-to-plant variation in these collections is evident in at least three features. Some plants have nearly glabrous ray-corollas; in others the ray-corollas are moderately or densely glandular. Some plants have nearly glabrous phyllaries; in others the phyllaries, especially the outer ones, are moderately or densely strigose. The apex of the phyllaries likewise is variable. In some plants the apices are broadly obtuse; in others they are acute, and in still others they are intermediate. Variety *montana* is ordinarily characterized by glabrous ray-corollas, and nearly glabrous or only lightly pubescent, obtuse phyllaries. The unusual characters in this population probably belong to *T. florifer*. The latter species has densely glandular ray-corollas and moderately strigose, acute phyllaries. It seems possible that pollen occasionally has been carried up to the *T. montana* population by insects which have visited *T. florifer* plants in the lower areas of adjacent Idaho.

Apomixis in var. *montana* is concentrated in the high-elevation, northernmost populations. This pattern is no different from that of the other species in the genus with abundant apomixis. Variety *minima* is so restricted that the geographic and altitudinal pattern of the range of its apomictic forms is not at present demonstrable. It should be noted that in one area (Red Canyon) apomicts and sexual plants of var. *minima* occur together.

8. *Townsendia mensana* M. E. Jones

Rosulate-pulvinate perennial with well-developed taproot; caudex developing few to numerous short, often subterranean, branches; leaves spatulate, oblanceolate or linear, entire, acute or slightly acuminate, mucronate, gray-strigose pubescent, often involute, up to 35 mm. long and 1-5 mm. wide; heads sessile or pedunculate; peduncles up to 3 cm. long, pilose-strigose; involucles often obconical at base, 6.5-17 mm. wide, 8.0-13.5 mm. high; phyllaries in 4-5 series, lanceolate to narrowly obovate, mostly acute, infrequently obtuse, with scarious or ciliate margins, glabrous to lightly strigose-pilose on the outer surface, 3.5-10 mm. long, 1.3-3.0 mm. wide; ray-florets ca. 12-30; ray-corollas whitish, pink or dull red, densely glandular on the abaxial surface, 7-12 mm. long, 1-2.3 mm. wide; disk-corollas yellow, often pink-tinged, 4-6 mm. long; achenes oblanceolate, compressed, 2-ribbed, those of the ray-florets sometimes 3-ribbed, moderately to heavily pubescent with duplex, glochidiate or bifurcate hairs; pappus of the ray- and disk-florets similar, of 15-35 plurisetose, barbellate bristles, 4.2-6.5 mm. long, or pappus of the ray-florets variously shortened. Reproduction sexual. Northeastern Utah to southeastern Nevada.

KEY TO THE VARIETIES

Leaves narrowly oblanceolate to linear, abaxial surface of leaf-bases densely woolly with long, white, multicellular trichomes; phyllaries lanceolate;

heads sessile, almost hidden in the tufts of leaves; plants of the Uinta Basin of Utah 8a. var. *mensana*.
Leaves oblanceolate to spatulate; abaxial surface of leaf-bases merely strigose with short trichomes; phyllaries broadly lanceolate to narrowly obovate; heads usually short-pedunculate, or if appearing sessile, not obscured by dense tufts of leaves; plants of western Utah and southeastern Nevada 8b. var. *Jonesii*.

8a. *Townsendia mensana* M. E. Jones var. *mensana*

Townsendia mensana M. E. Jones, Contr. West. Bot. 13: 15. 1910.
Type: *Jones s.n.*, benches of the Uintas, Theodore (now Duchesne), 7,500 ft. alt., Duchesne Co., Utah, 14 May 1908 (POM, holotype). Uinta Basin, Utah. Map 8. Plate XX, fig. 1.

Representative specimens. Utah. Duchesne Co.: 26 mi. southwest of Myton, 7000 ft. alt., *Barneby 12701* (*CAS); 15 mi. west of Duchesne, *Beaman 865* (GH); "bench" of the Uintas, 11 mi. north of Duchesne, *Beaman 868* (GH); 3 mi. west of Duchesne, 5500 ft. alt., *Ripley & Barneby 4677* (CAS). Uintah Co.: between Hill Creek and Green River, ca. 20 mi. south of Ouray, *Bartholomew & Bartholomew s.n.*, June 1955 (GH).

8b. *Townsendia mensana* M. E. Jones var. *Jonesii* Beaman, var. nov.

Type: *Jones s.n.*, Mammoth, 7000 ft. alt., Juab Co., Utah, 10 May 1910 (POM 39891, holotype).

Leaves oblanceolate or spatulate, acuminate, the bases strigose on the abaxial surface; heads mostly short-pedunculate. Western Utah and southeastern Nevada. Map 8. Plate XX, fig. 2.

Foliis oblanceolatis vel spatulatis, acuminatis, basi strigosis, capitulis plerumque breviter pedunculatis.

Representative specimens. Nevada. Clark Co.: Deer Creek, Charleston Mountain, 8250 ft. alt., *Alexander 774* (*UC); ridge south of Deer Creek, 2670 m. alt., *Clokey 7772* (UC); Lee Canyon, 2650 m. alt., *Clokey 7773* (UC); Hidden Forest Canyon, Sheep Range, 9500 ft. alt., *Munz 16836* (POM, UC). Lincoln Co.: Mt. Irish, 6000 ft. alt., *Jaeger s.n.*, 19 June 1938 (POM). White Pine Co.: Schellbourne, *Jones s.n.*, 13 July 1891 (POM). Utah. Juab Co.: McIntyre's Ranch, *Jones s.n.*, 18 May 1891 (POM); Silver City, *Jones s.n.*, 27 March 1896 (POM); Tintic Junction, 5500 ft. alt., *Jones s.n.*, 9 May 1910 (POM). Millard Co.: Leamington, 5000 ft. alt., *Jones s.n.*, 8 May 1911 (POM, atypical, hybrid with *T. florifer*?, cf. discussion); San Pete Co.: 2 mi. southeast of Ephraim, *Beaman 820* (GH); Gunnison, 5000 ft. alt., *Jones s.n.*, 18 April 1911 (POM). Sevier Co.: ridge between Cottonwood and Willow Creeks, 8000 ft. alt., *Robinette 105 L. R.* (*NA). Tooele Co.: Deep Creek, *Jones s.n.*, 6 June 1891 (POM). Tooele or Utah Co.: Mercur, 5500 ft. alt., *Jones s.n.*, 6 June 1896 (*MO, NY, POM, US, *UTC). Wayne Co.: 10 mi. southeast of Teasdale, *Beaman 822* (*GH).

This nearly unknown species has recently figured in a nomenclatorial confusion. It was placed in synonymy under *T. sericea* (=*T. Hookeri*) by Larsen (1927). Its resemblance to that species is superficial.¹ Cronquist first recognized that *T. sericea* is invalid as it included the type of the earlier *Aster ? exscapus* [=*Townsendia exscapa* (Richards.) Porter]. With *T. mensana* residing in synonymy under *T. sericea* in Larsen's treatment, it appeared that the epithet "mensana" should be taken up for the latter species. Both Cronquist (1955, pp. 326-327) and I (Beaman, 1954, p. 172) fell into a trap by not having seen the type of *T. mensana*. Critical study of the type and other material indicates that *T. mensana* must be recognized as a species in its own right.

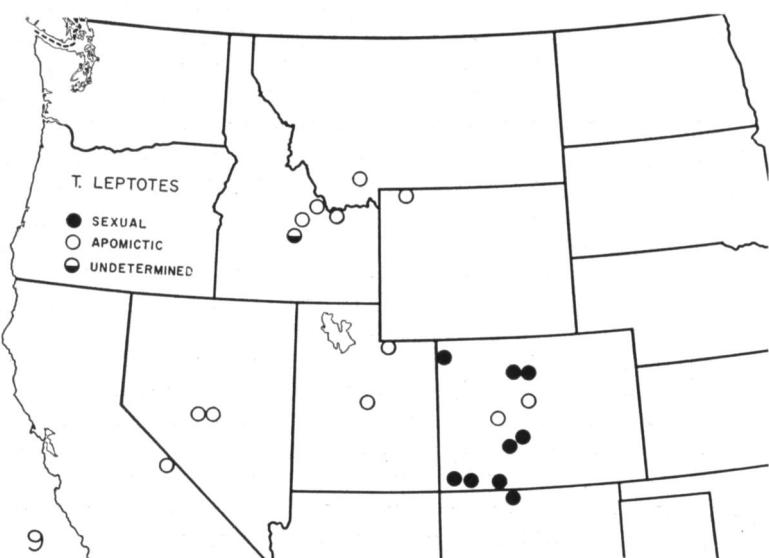
Townsendia mensana var. *mensana* is endemic to the Uinta Basin of Utah. From my field observations, it appears that the variety has its best development on the pinon- and juniper-covered "benches" of the Uintas to the north and west of Duchesne. It occurs also at slightly lower elevations, with a host of other specialized little xerophytes, on the white shales of the Green River formation.

Townsendia mensana var. *Jonesii* occurs over a wider area and is represented by many more specimens than is var. *mensana*. Marcus E. Jones, however, has been the principal collector of var. *Jonesii*, and the variety is named in his honor.

The diversity of *T. mensana* var. *Jonesii* is considerable. The plants of Utah mostly have narrow, oblanceolate leaves, the heads are borne on conspicuous peduncles, and the phyllaries are usually acute. The Nevada plants, on the other hand, mostly have broader, nearly spatulate leaves, the heads are nearly sessile, and the phyllaries are usually slightly obtuse. The variation between plants of the two areas is continuous, however, and it seems best to consider the material as a single taxon.

The variation trend of the Utah material of var. *Jonesii* is in the direction of *T. florifer*. For the most part this variation is subtle, and the present material is not adequate to permit a good understanding of its cause. Only two collections, *Jones s.n.*, 8 May 1911 (Millard Co., Utah) and *Jones s.n.*, 6 June 1891 (Tooele Co., Utah), show strongly intermediate characters between *T. florifer* and *T. mensana* var. *Jonesii*. Unfortunately both collections are scanty, one consisting of one small plant, the other of two. In the Millard County collection (2 plants), one plant seems nearer

¹ It should be noted that *T. Hookeri* has been collected by Marcus Jones near the type-locality of *T. mensana* var. *mensana*.



MAPS 8-9. 8. Geographic distribution of *Townsendia mensana* var. *mensana* and *T. mensana* var. *Jonesii*. 9. Geographic distribution of sexual and apomictic *T. leptotes*.

T. florifer, the other nearer *T. mensana* var. *Jonesii*. One plant has mostly glochidiate achenial hairs; the other has mostly bifurcate hairs. The plant with the bifurcate hairs appears to be annual or biennial; the other could be perennial. The phyllaries of both plants are in three series and similar to those of *T. florifer*. In the Tooele County specimen the achenial hairs are bifurcate, the phyllaries are in four series and have a strigose pubescence intermediate between typical *T. florifer* and typical *T. mensana* var. *Jonesii*. In general aspect this plant seems closer to typical *T. mensana* var. *Jonesii* than do the two Millard County plants.

This evidence of hybridization between *T. mensana* var. *Jonesii* and *T. florifer* is meager. However, in view of the general situation in *Townsendia* as regards interspecific hybridization, it would be surprising if crossing did not occur between the two. They occur sympatrically over a fairly large area in the sagebrush lands of west-central Utah. They probably occupy the same or at least very similar habitats. Marcus Jones (1893, p. 262) states that *T. mensana* var. *Jonesii* (det. by him as *T. scapigera*) is rare. Very likely it is, since he is the only collector of it in the area of probable hybridization. But even though it is rare, an intensive field investigation might be expected to demonstrate considerable gene interchange between *T. florifer* and *T. mensana* var. *Jonesii*.

The closest relationship of *T. mensana* appears to be with *T. montana*. The ancestral stock in the Wasatch region may have differentiated into low-elevation *T. mensana* and high-elevation *T. montana*. Some relationship between the two species is shown by the similar habit, the similar involucral bracts (especially between *T. montana* and the southern Nevada populations of *T. mensana* var. *Jonesii* which have broad, obtuse phyllaries), and the similar light pubescence of the phyllaries.

The differences between the two varieties of *T. mensana* are minor, although constant. The two taxa have been placed at the varietal level to indicate their very close morphological relationship. Variety *mensana* has probably been isolated in the Uinta Basin for sufficient time to become somewhat differentiated from a more primitive var. *Jonesii* stock.

9. *Townsendia leptotes* (A. Gray) Osterhout

Townsendia leptotes (A. Gray) Osterhout, Muhlenbergia 4: 69. 1908. [*leptotes* apparently a typographical error by Osterhout of Gray's epithet *leptotes*]. *T. sericea* Hook. var. *leptotes* A. Gray, Proc. Am. Acad. 16: 85. 1880. Type: *Parry s.n.*, Middle Park, Grand Co. (?),

Colorado, July-August 1864 (**GH*, holotype; *F*, *MO*, *NY*, *PH*, *UC*, *YU*, isotypes; *us*, probable isotype but dated 1862).

Rosulate-pulvinate perennial with well-developed taproot; caudex of few to numerous, short, subterranean branches terminated by tufts of leaves; leaves linear to oblanceolate or narrowly spatulate, entire, mucronate, thickish, usually involute, glabrous to rather heavily strigose-sericeous, up to 60 mm. long and 3.5 mm. wide; heads sessile or pedunculate, the peduncles not more than 2.8 cm. long; involucres campanulate, 0.8-2.3 cm. wide, 0.5-1.5 cm. high; phyllaries in 4-7 (rarely 3) series, lanceolate to linear, acute or rarely slightly rounded, ciliate and scarious-margined, glabrous or very lightly strigose on the outer surface, 3.5-12 mm. long, 0.5-2 mm. wide; ray-florets ca. 15-40; ray-corollas whitish, cream, pink, or blue, glabrous or nearly so, 8-14 mm. long, 1-2.5 mm. wide; disk-corollas yellow, sometimes pinkish-tinged, 3.2-7 mm. long; achenes oblanceolate, compressed, 2-ribbed, those of the ray sometimes 3-ribbed, lightly to moderately pubescent with long, thin, duplex, glochidiate hairs or glabrous with only a few basal hairs, sometimes papillose; pappus of the ray- and disk-florets similar, of plurisetose barbellate bristles, 3-8 mm. long, or pappus of the ray-florets variously shortened or absent. $2n = 18$ in sexual plants, and $2n = 27-36$? in apomictic plants (inferred from pollen measurements). Western Montana to central Idaho and south to northwestern New Mexico, central Nevada and east-central California. Map 9. Plate XX, figs. 3 and 4.

Representative specimens. **California.** Mono Co.: R. 34 E, T. 5 S. Sect. 2, White Mountains U. S. G. S. Map, 11,500 ft. alt., *Duran* 1661 (*†UC*); north slopes of Sheep Mountain, White Mountains, 12,000 ft. alt., *Maguire & Holmgren* 26109A (*UC*, *†UTC*). **Colorado.** Archuleta Co.: Pagosa Springs, *Bethel* s.n., 23 May 1917 (**cs*); hillsides, southeast of Pagosa Springs, 7200 ft. alt., *Ripley & Barneby* 7589 (**CAS*); Pagosa Springs, *Smith* s.n., 12 May 1894 (*PH*). Grand Co.: 4.5 mi. west of Kremmling, *Beaman & Preece* 513 (**ws*); Kremmling, *Osterhout* 5221 (**OKL*, *POM*, *RM*); 1 mi. east of Grandby, 7800 ft. alt., *Ripley & Barneby* 10586 (**CAS*). Gunnison Co.: crest of ridge between Avery Mountain and Virginia Mountain, near Gothic, *Beaman & Barclay* 799 (*†CH*); North Station Ridge near Gothic, 12,000 ft. alt., *Langenheim* 725 (*†COLO*, *cs*); Fairview Peak, 13,200 ft. alt., *Langenheim* 1292 (*†COLO*); Matchless Mountain, 12,000 ft. alt., *Langenheim* 1309 (*COLO*). Lake Co.: near Leadville, *Schedin & Schedin* 478 (**RM*). La Plata Co.: 5 mi. northwest of Hesperus, *Pennell* 21464 (**NY*, *PH*). Moffat Co.: saddle just west of fire lookout, summit of Roundtop Mountain, Dinosaur National Monument, 2800 m. alt., *Wolf & Dever* 5193 (**COLO*). Montezuma Co.: Mancos, *Eastwood* s.n., June 1891 (**POM*); Cortez, *Nelson* 10437 (*CH*, *MO*, *NY*, **RM*, *UC*). Park Co.: South Park, *Wolf & Rothrock* 418 (*†CH*, *NY*, *†us*). Saguache Co.: Marshall Pass., *Ferrill* s.n., 13 June 1903 (**cs*); Cochetopa Park, just south of summit of Cochetopa Pass, ca. 9600 ft. alt., *Weber* 9421 (*COLO*, **CH*). **Idaho.** Blaine Co.: Mt. Hyndman,

Sawtooth Range, 8000 ft. alt., *Thompson* 13626 (MO p.p., with 3 plants of *T. montana*). Clark Co.: 3 mi. from head of Medicine Lodge Creek, *Davis* 3148 (\dagger DS; \dagger NA p.p., with 1 plant of *T. Hookeri*). Custer Co.: Mt. Borah, Chilly, *Christ & Ward* 10424 (\dagger NY); southeast of Double Springs Summit, 8 mi. northeast of Dickey, 8500 ft. alt., *Cronquist* 3197 (\dagger CH, DS, MO, all p.p., with plants of *T. montana*); pass in mts. 7 mi. north of Dickey, 8500 ft. alt., *Hitchcock et al.* 3790 (\dagger WTU); mouth of Rock Creek, north slope, Lost River Mountains, *Hitchcock* 15725 (\dagger WTU). Lemhi Co.: Liberty Mountain, Lemhi Range, west of Gilmore, *Christ & Ward* 14886 (\dagger NY p.p., with 3 plants of *T. montana*); near head of Spring Canyon ca. 8 mi. southeast of Gilmore, Lemhi Mountains, *Hitchcock & Muhlick* 9317 (NY, \dagger WTU). **Montana.** Madison Co.: without definite locality, 9500 ft. alt., *Tweedy* 229 (\dagger NY). **Nevada.** Nye Co.: summit above Pine Creek Basin, Toquima Range, 11,300 ft. alt., *Maguire & Holmgren* 25818 (\dagger NY, UC, UTC); summit extending northeast, 1 mi. from Toiyabe Dome, 10,500 ft. alt., *Maguire & Holmgren* 25944 (CAS, \dagger NY, UC, UTC). **New Mexico.** Rio Arriba Co.: hills south of village, Tierra Amarilla, 2300 m. alt., *Eggleson* 6444 (F, *GH, *MO, NY, US). **Utah.** San Pete Co.: Spring Hollow Drainage above Great Basin Experiment Station, Manti National Forest, 10,200 ft. alt., *Holmgren & Shaw* 7640 (\dagger UC, UTC). Summit Co.: ridge east of East Fork of Bear River, Uinta Mountains, 11,400 ft. alt., *Goodman & Payson* 450 (OKL, \dagger RM); divide between East Fork of Bear River and Black's Fork, Uinta Mountains, 10,500 ft. alt., *Goodman & Hitchcock* 1517 (DS, F; GH p.p., with 1 plant of *T. montana*; MICH, \dagger MO, MONTU, \dagger NY p.p., with 2 plants of *T. montana*; PH, RM, UC). **Wyoming.** Fremont Co. (?): gravelly hills, Wind River Mts., *Hayden* s.n., 15 May 1860 (\dagger MO). Yellowstone National Park: Saddle Mountain, 10,000 ft. alt., *Tweedy* 697 (\dagger CH, NY).

Townsendia leptotes exhibits the greatest interpopulation variation of any species in the genus. No two collections from sexual populations are entirely similar. Variation occurs even between populations which are only a short distance apart. The species is most diversified in western Colorado.

Sexual populations of *T. leptotes* appear to be confusing and difficult to determine, mostly as a result of hybridization with *T. exscapa*. The populations of southwestern Colorado and adjacent Rio Arriba County, New Mexico exhibit a polymorphy which seems attributable only to the influence of *T. exscapa*. In southwestern Colorado *T. leptotes* becomes a large plant with a much-branched caudex; it has relatively large, sessile heads with involucres averaging ca. 2.0-2.5 cm. wide; the disk-corollas are unusually long, averaging 5.5-6 mm., and the disk-pappus is

correspondingly long. These atypical features of *T. leptotes* are characteristic of *T. exscapa*.

An unusual character, not from *T. exscapa*, in the southwestern Colorado material of *T. leptotes* is the short ray-pappus. *Townsendia glabella*, which occurs in that area also, has a short ray-pappus. However, no other features definitely suggest gene exchange between these two species. This character could have had an independent development in the southwestern Colorado populations of *T. leptotes*. As the ray-pappus is a variable character in several other *Townsendia* species, such an explanation might apply here.

The polymorphy between populations of the apomicts of *T. leptotes* indicates that apomixis must have occurred independently in several different sexual populations. For this reason the apomicts are interesting from a phytogeographic point of view. Those of the Uinta Mountains (e.g., *Goodman & Hitchcock* 1517) are very similar to the plants of southwestern Colorado. They have the short ray-pappus and the habit almost exactly duplicates that of the purer (relatively undiluted with *T. exscapa*) sexual plants of southwestern Colorado (e.g., *Ripley & Barneby* 7589). The apomicts of Park County, Colorado (*Wolf & Rothrock* 418) are very similar to sexual *T. leptotes* from Marshall Pass, Saguache County, Colorado (*Ferril s.n.*, 13 June 1902). The apomicts of San Pete County, Utah, Nye County, Nevada, and Mono County, California (e.g., *Holmgren & Shaw* 7640, *Maguire & Holmgren* 25944 and *Maguire & Holmgren* 26109A, respectively) are more difficult than the preceding examples to relate to a known sexual type but they are morphologically close to some of the alpine apomicts from Gunnison County, Colorado (e.g., *Beaman & Barclay* 799). The Idaho apomicts are closest morphologically to the apomicts of the Uinta Mountains of Utah, but in the Idaho material (in contrast to the Uinta material with the short ray-pappus) the ray-pappus is about as long as that of the disk.

In Wyoming *T. leptotes* is known only from apomicts of two old collections (*Tweedy* 697 and *Hayden* s.n., 15 May 1860). These are perplexing because of their resemblance to *T. spathulata*. Their narrow phyllaries and glabrous achenes are characters of *T. leptotes*. Their pubescence is nearly as dense as that of *T. spathulata*, and their pappus is deciduous like that of *T. spathulata*. The oblanceolate leaves are about intermediate between the two species. These plants could be apomictic hybrid derivatives of *T. leptotes* and *T. spathulata*. Further field studies of the

populations in western Wyoming are needed to help clarify the relationship that seems to exist between these two species.

Putative hybridization between *T. montana* var. *montana* and *T. leptotes* in the Uinta Mountains has been considered in the discussion of the former species. It is possible that the Idaho apomicts of *T. leptotes* are hybrid derivatives of these two species. In Idaho the two are so similar that previously they both have been referred to *T. montana*. Their similarity is apparent from the mixed collections in which they occur (*Christ & Ward* 14886, *Cronquist* 3197, and *Thompson* 13626).

10. *Townsendia Hookeri* Beaman, sp. nov.

Type: *Clokey* 4338, dry hills, Mt. Vernon Canon, 1730 m. alt., Jefferson Co., Colorado, 13 April 1920 (*COLO 12061, holotype; CAN, CAS, DS, F, GH, MICH, MO, MONTU, NA, PH, POM, *RM, UC, US, UTC, WS, WTU, isotypes).

Densely rosulate-pulvinate perennial with well-developed taproot; caudex of few to numerous short, subterranean branches, appearing smooth with the matted pubescence of the old, persistent leaf bases, the branches terminated by tufts of leaves and frequently by a flowering head; leaves linear to narrowly oblanceolate, entire, acute, mucronate, involute, thickish, densely strigose-sericeous, up to 45 mm. long and 2 mm. wide (rarely up to 3.5 mm. wide); heads sessile (rarely short-pedunculate on peduncles up to 1.3 cm. long) at the ends of the caudex branches, embedded in and surpassed by the tufts of leaves; involucres obconical-campanulate, 8-18 mm. wide, 9-15 mm. high; phyllaries in 5-7 (rarely 3-4) series, linear or nearly so, acute or acuminate, mostly terminated by a tuft of tangled cilia, ciliate and scarious-margined, the outer phyllaries sometimes glandular on the lower margin, nearly glabrous to pilose-strigose on the outer surface, purplish upward, 5-13 mm. long, 0.6-1.8 mm. wide; ray-florets ca. 15-30; ray-corollas white on the adaxial surface, the abaxial surface cream or pinkish, glabrous or nearly so, 8.5-14 mm. long, 1-2.5 mm. wide; disk-corollas yellow, sometimes pinkish-tipped, 4.0-6.5 mm. long; achenes oblanceolate, compressed, 2-ribbed, pubescent with long, thin, duplex, glochidiate hairs, sometimes papillose, 3.5-4.7 mm. long, 1.0-1.4 mm. wide; ray-pappus variable, of very short plurisetose bristles ca. 1 mm. long or of plurisetose, barbellate bristles up to 5.5 mm. long or with both long and short bristles on the same achene; disk-pappus of plurisetose, barbellate bristles 5-8.2 mm. long, exceeding at least slightly the length of the disk-corollas. $2n = 18$ in sexual plants and $2n = 27-36$? in apomictic plants (the latter inferred from pollen measurements). Northeastern British Columbia south to southern Colorado and central Utah. Map 10. Plate XVII and Plate XX, figs. 5 and 6.

Herba perennis pulvinata; radix fusiformis; ramosis caudicis paucis vel numerosis; folia linearia ad suboblanceolata, integerrima, strigoso-sericea, ad 4.5 cm. longa et 2 mm. lata. Capituli in summo caudicis sessiles; involucrum 8-18 mm. latum, 9-15 mm. altum; involucri squamis plerumque 5-7 seriatis, lineari-subulatis, acutis vel acuminatis, 5-13 mm. longis, 0.6-1.8 mm. latis.

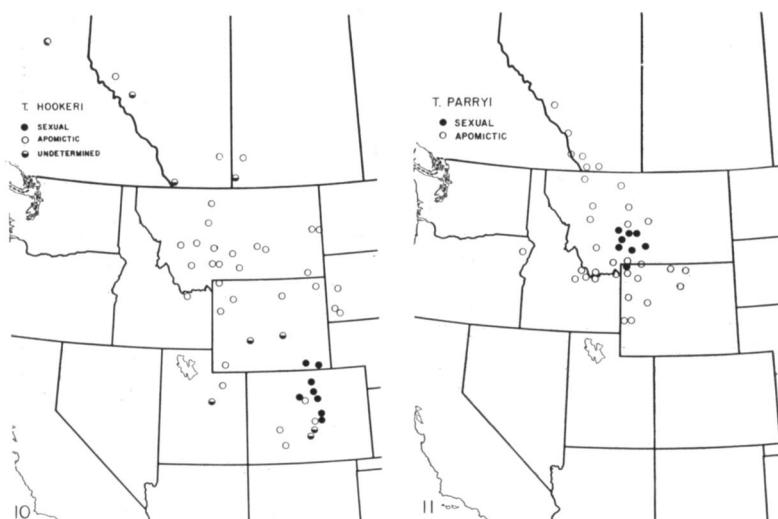
Corollae radiorum 8.5-14 mm. longae, 1-2.5 mm. latae; corollae disci 4.0-6.5 mm. longae. Achaenia oblanceolata, compressa, pubescentia cum pilis glochidiatis, 3.5-4.7 mm. longa, 1.0-1.4 mm. lata; radiorum pappo ca. 1 mm. longo vel usque 5.5 mm. longo; disci pappo plurisetoso, 5-8.2 mm. longo.

Representative specimens. CANADA. Alberta. Rocky Mountains, *Drummond* 573 (\dagger CAN); Sweet Grass Hills, *Macoun* 10897 (CAN, ND); Waterton Lakes National Park, hilltop near north park entrance, 4200 ft. alt., *Breitung* 17067 (NY); Banff National Park, upper drainage of N. Saskatchewan River, Valley of Mistaya River, between Saskatchewan Crossing and Waterfowl Lakes, 4500 ft. alt., *Porsild* & *Breitung* 14758 (CAN, GH); Medicine Hat, *Spreadborough* 5027 (CAN, \dagger GH, MO, NY, US). British Columbia. Fort McLeod, *Cowdry* 7709 (CAN). Saskatchewan. Cypress Hills, summit of hills east of Boyd's Ranch, *Breitung* 5357 (DAO); Maple Creek, *Campbell* 129 (\dagger DAO p.p., with 1 plant of *T. exscapa*). UNITED STATES. Colorado. Boulder Co.: near Boulder, *Ramaley* 654 (COLO, *RM); $\frac{1}{2}$ mi. east of Hi-Way Mine, 3 mi. south of LaFayette, *Weber* 3713 (COLO, p.p., with 1 plant of *T. exscapa*). Clear Creek Co.: Georgetown, *Wolf* & *Rothrock* 416 (F, \dagger GH; US p.p., with 1 plant of *T. leptotes*). Custer Co.: high mountain valley, *Cusack* s.n., 1888 (F); Denver Co.: Denver, 5000 ft. alt., *Bethel* s.n., 1 May 1894 (*NY; US p.p., with 1 plant of *T. exscapa*). Fremont Co.: Canon City, *Brandegee* 41 (*? PH p.p., with 2 plants of *T. exscapa*). Gilpin Co.: Central City, *Scovell* s.n., 1869 (*MICH). Gunnison Co.: Sabinero, *Wheeler* 598 (COLO: \dagger RM p.p., with 2 plants of *T. exscapa*). Larimer Co.: Foothills (Fort Collins), *Crandall* 305 (*US p.p., with 3 plants of *T. exscapa*); Horse-tooth Gulch, *Crandall* 3131 (CS, *NY, RM, YU). Mineral Co.: the "Mesa", Creede, Rio Grande National Forest, 8900 ft. alt., *Murdock* 4503 (DS, F, \dagger MO, US). Idaho. Clark Co.: 3 mi. from head of Medicine Lodge Creek, Range 31 E., Twp. 13 N., *Davis* 3148 (\dagger NA p.p., with 2 plants of *T. leptotes*). Montana. Cascade Co.: Great Falls, *Anderson* 203 (\dagger MONTU, YU). Dawson Co.: Glendive, *Temple* s.n., 30 April 1952 (\dagger MONT). Gallatin Co.: Bozeman, *Tweedy* s.n., May 1882 (\dagger NY). Granite Co.: east of Drummond, *Rose* 30 (\dagger MO, MONTU, WS). Lewis & Clark Co.: Helena, *Kelsey* s.n., April 1888 (DS, \dagger POM, UC). Liberty Co.: Cottonwood Coulee, ca. 20 mi. southeast of Chester, *Marks* s.n., 4 May 1946 (\dagger WS). Madison Co.: Silver Star, *Fitch* s.n., May 1893 (\dagger NY). Musselshell Co.: Musselshell City (or Round-up or Petroleum City) *Wickland* s.n., 28 May 1936 (N.Y.A. Project) (\dagger MONTU). Meagher Co.: 9 mi. south, 5 mi. west of White Sulphur Springs, *Wright*, *Cash* & *Booth* 5469 (\dagger MONT). Park Co.: 8 mi. west of Livingston, *Booth* s.n., 9 May 1948 (MONT, MONTU, \dagger RM). Powder River Co.: 6 mi. west of Boyes, *Anderson* & *Scharff* s.n., 23 April 1952 (\dagger MONT). Powell Co.: Deer Lodge, along Spencer Creek, *Kirkwood* 1360 (\dagger GH, MONTU). Stillwater Co.: Absarokee, *Hawkins* s.n., 20 April 1919 (\dagger MONT). Sweetgrass Co.: northeast corner of county, *Anderson* & *Scharff* s.n., 21 April 1952 (\dagger MONT). Wibaux

Co.: Wibaux, *Blankinship* 1503 (\dagger MONT). Yellowstone Co.: 7 mi. south of Custer Station, Northern Pacific Railway, Big Horn River, *Blankinship* 147 (\dagger MO, MONT, us). South Dakota. Custer Co.: Pringle, Black Hills National Forest, 4900 ft. alt., *Murdock* 3510 (F, GH, \dagger NY). Fall River Co.: 5 mi. southwest of Buffalo Gap, *McIntosh* 18 (\dagger DAO, RM). Meade Co.: Black Hills, near Ft. Meade, *Forwood* 93 (\dagger us). Utah. Carbon Co.: Scofield, *Jones* s.n., 24 June 1904 (POM). Duchesne Co.: Theodore (now Duchesne), benches of the Uintas, 8000 ft. alt., *Jones* s.n., 13 May 1908 (\dagger POM). Wyoming. Albany Co.: ca. 12 mi. southeast of Laramie on U. S. Rt. 30, ca. 8800 ft. alt., *Beaman & Preece* 508 (*ws); Laramie, *Nelson* 7055 (MO, NY, POM, *RM, us). Crook Co.: hillsides near Hulett, 4000 ft. alt., *Ownbey* 526 (COLO, GH, IDS, \dagger MO, MONTU, NY, RM, UC, UTC, WS, WTU). Fremont Co.: 1 mi. south of Pacific Creek, *Beaman* 884 (GH). Fremont Co. (?): Pilot Knob, *Hobbs* 5 (\dagger PH). Johnson Co.: hillsides about 8 mi. west of Buffalo, *Rollins* 408 (MO, NY, \dagger WS). Laramie Co.: bluffs near Cheyenne, *Havard* 10 (*NY). Natrona Co.: 4 mi. west of Alcova, *Beaman* 877 (GH). Natrona Co. (?): southwest end of Bate's Hole, *Payson & Payson* 4738 (\dagger RM). Park Co.: Shoshone Mountains, *Hapeman* s.n., May 1907 (\dagger MO). Teton Co.: 11 mi. north of Jackson, ca. 6200 ft. alt., *Beaman & Preece* 506 (ws); Black Tail Butte, Moose, *Craighead* s.n., 25 May 1947 (\dagger IDS). Uinta Co.: near Lyman, 6500 ft. alt., *Rollins* 1619 (GH, \dagger NY). Yellowstone National Park: Hills near Mammoth Hot Springs, 6200 ft. alt., *Burglehaus* s.n., May 1893 (\dagger us, WTU).

Larsen (1927) recognized that Hooker had included two specific elements in his species, *Townsendia sericea*, upon which he based the genus. She did not recognize, however, that *T. sericea* was invalid because it included the type of the earlier *Aster* ? *exscapus* (cf. Beaman, 1954, Cronquist, 1955, and the discussion of *T. mensana* in the present paper). Thus, the element which was not *Aster* ? *exscapus* [*Townsendia exscapa* (Richards.) Porter] was not described by her. The "new" species, *T. Hookeri*, is named in honor of the founder of the genus *Townsendia*.

To the layman, *T. Hookeri* is perhaps as well known as any species of *Townsendia*. In Colorado it is abundant at the base of the Front Range and is one of the first flowers of the year; hence, its name Easter Daisy (applied also to *T. exscapa*). The botanists' confusion of *T. Hookeri* and *T. exscapa* is a result of the great similarity of the two, which may have resulted from extensive hybridization. In addition, over most of their ranges from Wyoming and Nebraska northward, both species reproduce only apomictically. Some specimens are easy to distinguish, but others are more intermediate and may be distinguished only with difficulty.



MAPS 10-11. 10. Geographic distribution of sexual and apomictic *Townsendia Hookeri*. 11. Geographic distribution of sexual and apomictic *T. Parryi*.

In southeastern Wyoming and the Front Range of Colorado sexual *T. Hookeri* and sexual *T. exscapa* occur together. I have not seen the two growing side by side, but several mixed collections such as *Bethel s.n.*, 1 May 1894, *Brandegee 41*, *Crandall 305*, *Rydberg & Vreeland 5408*, and *Weber 3713*, indicate that they must grow very close together. Their flowering periods at least partly coincide (both species of the plants of the mixed collections are in flower), and thus conditions to permit hybridization appear favorable. The nature of variation of plants of both species strongly suggests that hybridization has occurred. Field studies should be made to permit a better understanding of the frequency of hybridization and introgression, which, from herbarium material, appear to be important in these two species. As an aid to field population studies, the important characteristics of the pure *T. Hookeri* and *T. exscapa* populations are compared in the table below.

Although the dates of collection of the mixed collections of *T. Hookeri* and *T. exscapa* from the Front Range of Colorado indicate that the two do flower at the same time, they may be at least partly isolated by differences in flowering period. Dr. Marion Ownbey (in conversation) has indicated that he found *T. Hookeri* (*Ownbey 526*, apomictic) in flower on April 27 and noted that

<i>T. Hookeri</i>	<i>T. exscapa</i>
CAUDEX branches very short, or in old plants becoming longer and thicker, appearing smooth to the unaided eye with the matted pubescence of old leaf bases.	CAUDEX branches short, or becoming longer in old plants, but not conspicuously thickened, the leaf bases less pubescent and more completely deciduous than in <i>T. Hookeri</i> , thus the branches without the superficially smooth texture of <i>T. Hookeri</i> .
LEAVES linear or very narrowly oblanceolate, involute, sericeous-canescens.	LEAVES oblanceolate to narrowly spatulate, not involute, strigose.
HEADS relatively small, sessile, the involucres ca. 1.5 cm. wide.	HEADS relatively large, frequently short-pedunculate, the involucres ca. 2.2 cm. wide.
PHYLLARIES linear-subulate, with a tuft of tangled cilia at the apex.	PHYLLARIES mostly narrowly lanceolate, without a tuft of cilia at the apex.
ACHENES moderately to densely pubescent.	ACHENES moderately to densely pubescent.
DISK-COROLLAS ca. 5 mm. long.	DISK-COROLLAS ca. 9-10 mm. long.
DISK-PAPPUS barely exceeding the length of the disk-corollas.	DISK-PAPPUS conspicuously longer than the disk-corollas.

other rather similar plants at the same locality were still in bud. He returned to this locality on May 6 and collected the later-flowering plants which proved to be *T. exscapa* (*Ownbey* 534, apomictic). The behavior of these apomicts may indicate that the flowering periods of their sexual precursors are slightly different.

Townsendia Hookeri is closely related to *T. leptotes*. This relationship is evident from a number of characters common to both species. Both have linear or at least very narrowly lanceolate leaves; in both, the phyllaries are very narrow. The habit of both is similar, and the two have a flowering period closely correlated with the beginning of spring. *Townsendia Hookeri* may have differentiated from a stock close to the present *T. leptotes*, as a result of isolation of populations on the two sides of the Front Range in Colorado.

The center of diversity of *T. exscapa* is to the south of Colorado. It probably was well-differentiated from *T. Hookeri* or the prototype of *T. Hookeri* before the two jointly occupied the area east of the Front Range in Colorado. It is possible, although entirely speculative, that the adaptation of *T. exscapa* to the Great Plains area has been coupled, through hybridization and apomixis, with the specialization of *T. Hookeri* to a colder environment. A combination of these two characteristics in the apomicts of both species may have permitted their migration far into the plains of Canada. It must be pointed out, of course, that some of the apomicts of the northern regions seem to have most of the characteristics of the pure species. This is particularly true of the apomicts of *T. Hookeri* in Montana. In that area they are more easily dis-

tinguished from *T. exscapa* than are some sexual *T. Hookeri* plants in Colorado. Of the two species, *T. exscapa* appears to be the one more markedly affected by hybridization.

Townsendia Hookeri is especially difficult to culture in the greenhouse as it merely develops buds which abort before they reach the meiotic stage. A cold treatment of at least two or three months is required to induce preformed buds to continue development and flower. When this species was first collected by Drummond he noted this characteristic. In so far as I know, it has never since been mentioned. Drummond stated (1829, p. 206): "It has a very singular habit, little like that of the genus *Aster* [he considered it to be Richardson's *Aster* ? *exscapus*]; the flower buds are formed in Autumn, and bear an exact similarity to those of *Globularia vulgaris*." Drummond was disappointed in the small, inconspicuous rays. Many apomicts, and his was one, have rays which do not fully expand.

The geographic pattern of sexual-apomictic distribution of *T. Hookeri* is a nearly diagrammatic one. The sexual forms occupy a limited area at the southern portion of the range. The apomicts, on the other hand, seem to be excluded from the immediate area where the sexual plants occur (except for high-elevation apomicts) but are widely distributed to the north.

11. *Townsendia exscapa* (Richards.) Porter

Townsendia exscapa (Richards.) Porter, Mem. Torr. Bot. Club 5: 321. 1894. *Aster* ? *exscapus* Richards. Frankl. Journ. Bot. App. 748. 1823. *Townsendia sericea* Hook. Fl. Bor.-Am. 2: 16. 1834. Type: Richardson s.n., Carleton House, Saskatchewan (†K, holotype).

Townsendia sericea Hook. β *papposa* A. Gray, Mem. Am. Acad. 4 (Pl. Fend.): 69. 1849. Type: Fendler 349, arid hillsides, less frequent in grassy places, Santa Fé, Santa Fé Co., N. Mex., April-May 1847 (*CH, holotype; NY, PH, UC, US, isotypes).

Townsendia Wilcoxiana Wood, Bull. Torr. Bot. Club 6: 163. 1877. *Townsendia exscapa Wilcoxiana* (Wood) Nels. in Coulter & Nels. Man. Bot. Rocky Mts. 510. 1909. Type: *Wilcox* s.n., Camp Supply, Indian Territory (Oklahoma, Woodward Co.), March 1877 (us, holotype).

Townsendia intermedia Rydb. in Britt. Man. 944. 1901. Type: Rich 718, Prairie, Trego Co., Kansas, 1896 (*NY, holotype; GH, MO, RM, US, isotypes).

Rosulate, taprooted perennial; caudex developing several short (or rarely elongated), often subterranean, branches, becoming woody; leaves oblanceolate, sometimes only narrowly so, entire, mucronate, strigose or strigose-sericeous, up to 8 cm. long, averaging ca. 3-3.5 cm., and up to 0.6 cm. wide, rarely with the widest less than 2 mm. wide; heads sessile

or short-pedunculate (in the southern portion of the range), the peduncles rarely more than 3 cm. long; involucres 1.3-3.7 cm. wide, 1-2.2 cm. high; phyllaries in 4-7 series, lanceolate or linear, acute or rarely obtuse, scarious-ciliate-margined, glabrous or lightly strigose on the outer surface, 5-14 mm. long, 1-3.9 mm. wide; ray-florets ca. 20-40; ray-corollas white or pinkish, often with a darker pink, longitudinal stripe on the abaxial surface, glabrous, 12-22 mm. long, 1-3 mm. wide; disk-corollas yellow, often pink- or purple-tipped or tinged, 6-11 mm. long; achenes oblanceolate or elliptic, compressed, 2-ribbed, those of the ray rarely 3-ribbed, moderately to heavily pubescent with long (or rarely short), duplex, glochidiate (or rarely only very slightly forked) hairs, if papillose only very inconspicuously so, 3.7-6.5 mm. long, 1.0-2.2 mm. wide; pappus of the disk and ray similar, of ca. 20-45 slender, plurisetose, barbellate bristles, 6-13 mm. long, that of the ray usually slightly shorter than that of the disk. $2n = 18$ in sexual plants and $2n = 27-36$? in apomictic plants (the latter inferred from pollen measurements). Central Manitoba to southwestern British Columbia and south to northern Mexico and southern Arizona. Map 12. Plate XVII and Plate XXI, fig. 1.

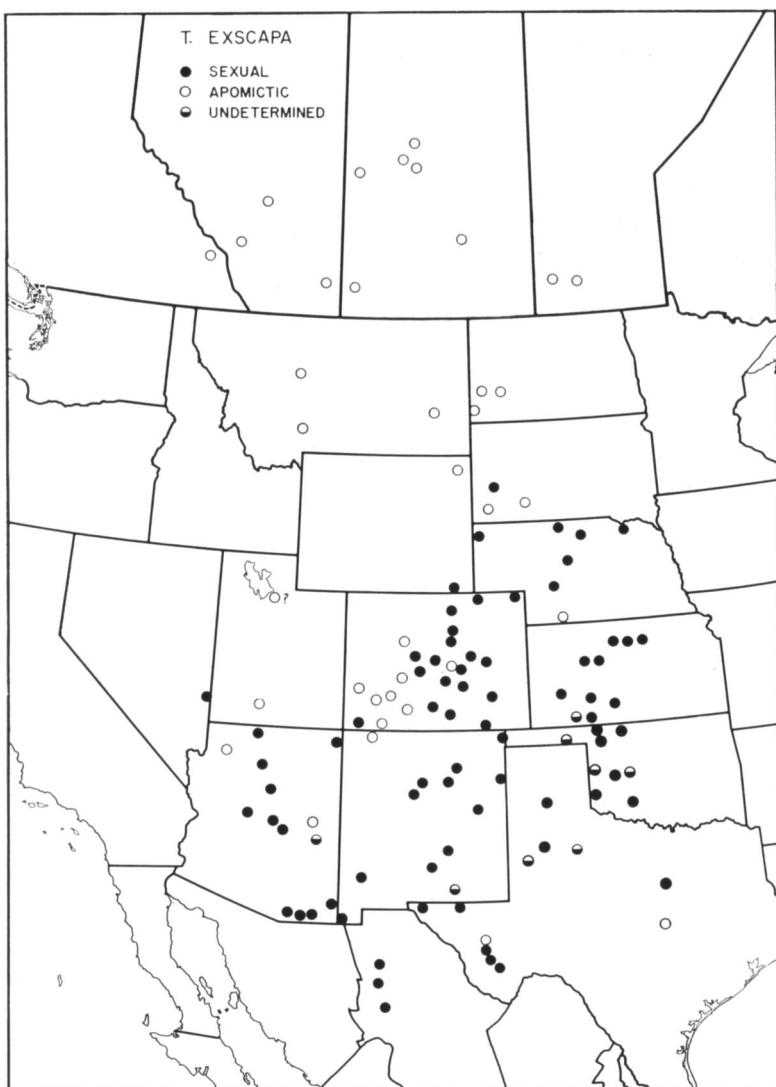
Representative specimens. CANADA. Alberta. Briggs Creek, Elbow River, *Macoun* 22787 (\dagger CAN); Rosedale Coulee, 2200-2500 ft. alt., *Moodie* 839 (F, \dagger GH, US); Medicine Hat, *Spreadborough* 5026 (\dagger CAN). British Columbia. 3 mi. north of Athalmer, *McCabe* 6133 (\dagger UC). Manitoba. Aweme, *Criddle* 900 (\dagger DAO, MO); hills southwest of Routledge, 7 mi. east of Virden, *Scoggan* 11187 (CAN). Saskatchewan. Maple Creek, *Campbell* 129 (\dagger DAO p.p., with one plant of *T. Hookeri*); Qu'Appelle Valley, *Carmichael R-10* (\dagger DAO); 8 mi. south, 1 mi. west of Saskatoon, near Beaver Creek, *Frankton* 1132 (\dagger DAO); $\frac{1}{2}$ mi. north of North Saskatchewan River, on Highway 5 near Ceepee, *Frankton* 1300 (\dagger DAO); Langham, *Fraser* s.n., 24 May 1938 (\dagger DAO); Broadacres, *Harrison* s.n., 1919 (\dagger DAO). MEXICO. Chihuahua. vicinity of Madera, 2250 m. alt., *Palmer* 315 in 1908 (*US); vicinity of Miñaca, *Rose* 11636 (*US); Puerta de St. Diego, 6500 ft. alt., *Hartman* 591 (*CH, US); Puerta de St. Diego, 6500 ft. alt., *Hartman* 641 (*CH). UNITED STATES. Arizona. Apache Co.: near Roof Butte, north end of Tunicha Mts., 2800 m. alt., *Goodman & Payson* 2912 (NA). Cochise Co.: west slopes, Burro Mts., *Maguire* 11575 (GH, *NY, UTC, WS, WTU); Huachuca Mts., *Orcutt* 57 (*UC); Chiricahua Mts., *Price* s.n., 8 April 1894 (*DS). Coconino Co.: Jacob Lake, 7925 ft. alt., *Barkley & Reed* 4372 (GH, *MONTU, NA); 1 mi. south of camp-grounds at Park Headquarters, Grand Canyon National Park, *Jones* 800 (*WS); vicinity of Flagstaff, 7000 ft. alt., *MacDougal* 31 (F, CH, NY, PH, RM, UC, US). Gila Co.: near North Peak, Matzatzal Mts., 1200 m. alt., *Collom* 290 (GH, MICH, *MO); near Payson, *Nelson & Nelson* 2004 (RM); 12 mi. north of Reynolds Creek, Sierra Ancha, 5600 ft. alt., *Peebles* 13269 (CH, NY). Mohave Co.: Uinkaret Plateau in vicinity of Mt. Emma, Grand Canyon National Monument, Toroweap, 7200-7600 ft. alt., *Cottam* 13982 (CAS, \dagger UT). Navajo Co.: roadside near Showlow, *Foster & Arnold* 285 (\dagger CH); Fort Apache, *Shuttleworth* s.n., 1892 (US). Santa Cruz Co.: hills between Patagonia and Sonoita,

Nelson & Nelson 1582 (GH, PH, RM, UC, US, UTC, ws); Sonoita, 4800 ft. alt., *Peebles & Fulton* 11473 (CAS, F, *GH, MICH, NY, POM). Yavapai Co.: just north of Prescott, 5200 ft. alt., *Barkley* 4313 (NA); Prescott, *Palmer* 601 in 1876 (*GH, MO, YU). Colorado. Adams Co.: 9 mi. north of Denver, 5500 ft. alt., *Gierisch* 865 (*UTC). Alamosa Co.: Morris Gulch, Great Sand Dunes National Monument, 8350 ft. alt., *Bean* 51-7 (*COLO). Boulder Co.: ½ mi. east of Hi-Way Mine, 3 mi. south of LaFayette, *Weber* 3713 (COLO p.p., with 3 plants of *T. Hookeri*). Chaffee Co.: 19 mi. south of Granite, *Beattie* 13 (*ws); Buena Vista, *Harper* (?) s.n., May 1886 (*COLO); 2 mi. south of Antero Junction, 9200 ft. alt., *Weber & Livingston* 6138 (*COLO). Denver Co.: Denver, *Eastwood* s.n., May 1888 (*POM); plains near Denver, 1500 m. alt., *Rydberg & Vreeland* 5409 (cs, *NY, *RM). Eagle Co.: Eagle, *Osterhout* 4704 (NY, †RM). Elbert Co.: 14 mi. east of Elbert, 6000 ft. alt., *Weber* 5980 (*COLO). El Paso Co.: plains, Colorado Springs, *Jones* 25 (NY, *POM, UTC); range pasture near Ramah, 6500 ft. alt., *Lamm* 19389 (CAN, *RM); near Colorado City, 6100 ft. alt., *Moldenke* 8192 (†NY); mesas near Colorado Springs, *Rydberg & Vreeland* 5408 (*NY p.p., with 2 plants of *T. Hookeri*). Fremont Co.: Canon City, *Brandegee* 41 (*NY; *PH p.p., with 1 plant of *T. Hookeri*). Gunnison Co.: near Gunnison, 7700 ft. alt., *Langenheim* 1227 (†COLO); Sapinero, *Wheeler* 598 (†RM p.p., with 2 plants of *T. Hookeri*). Hinsdale Co.: Lake City, *Pease* s.n., 16 May 1878 (†NY, †us). Huerfano Co.: hills southeast of La Veta, 2200-2300 m. alt., *Rydberg & Vreeland* 5407 (*NY, *RM). Lake Co.: Malta Station near Leadville, *Osterhout* 3197 (*RM). La Plata Co.: Los Pinos (Bayfield), *Baker* 730 (F, GH, MO, ND, NY, POM, †RM, us). Larimer Co.: foothills, (Ft. Collins), 6000 ft. alt., *Crandall* 305 (*us p.p., with 3 plants of *T. Hookeri*); plains near foothills, Ft. Collins, *Crandall* 3132 (cs; *MONTU p.p., with 1 plant of *T. Hookeri*; NY, RM, US, YU); foothills west of Ft. Collins, *Preston* s.n., 28 April 1921 (*cs). Las Animas Co.: hillside about 1 mi. south of western end of Mesa de Maya, *Rogers* 5647 (*COLO). Lincoln Co.: 17 mi. south of Limon, Highway 71, Middle Rush Creek, *Maslin* s.n., 28 April 1951 (*CAS, COLO, DAO, *RSA, WS, WTU). Montezuma Co.: below camp-ground, Spruce Canyon, Mesa Verde National Park, *Mathias* 668 (*MO, POM). Montrose Co.: hillside, Naturita, 6000 ft. alt., *Payson* 326 (COL, GH, †MO, RM). Otero Co.: 5 mi. east of La Junta, 4100 ft. alt., *Harrington* 2494 (*cs). Park Co.: Glentivar, in basin, *Christ* 224 (*cs). Pueblo Co.: sides of gulches about Pueblo, *Woodward* s.n., 1883 (GH, *YU). Rio Grande Co.: hillside just south of Beaver Creek Campground, Rio Grande National Forest, west of South Fork, 8200 ft. alt., *Weber & Livingston* 6205 (†COLO). San Miguel Co.: Telluride, *Eastwood* 5259 (†CAS). Sedgwick Co.: vicinity of Ovid, *Weber* 6037 (*COLO). Weld Co.: Pawnee Buttes, *Mattoon* s.n., 3 April 1953 (*COLO); Windsor, *Osterhout* 932 (NY, *RM); vicinity of New Windsor, *Osterhout* s.n., 11 May 1899 (F, NY, *RM). Kansas. Clark Co.: with-

out definite locality, *Curtis s.n.*, (*MO). Ellis Co.: 2½ mi. east of Hays, *Bondy* 513 (CAN, F, *MO, WTU); hills 2 mi. west of Hays, *Runyon* 319 (CM, PH, *RM). Finney Co.: Garden City, *Bennett* 69 (*RM). Ford Co.: Spearville, collector unknown, 27 April 1886 (*us). Meade Co.: Meade, *Smyth* 129 (us). Mitchell Co.: without definite locality, *Carleton s.n.*, April 1888 (ILL, *YU). Osborne Co.: hills within a radius of 5 mi. of Osborne City, *Shear* 2 (GH, MO, NY, RM, *us). Pratt Co.: slope near Cullison, *Norris s.n.*, 31 March 1888 (*MO). Trego Co.: prairie, *Rich* 718 (GH, MO, *NY, RM, us). **Montana.** Cascade Co.: Sand Coulee, *Anderson s.n.*, May 1888 (†MONTU). Custer Co.: U.S.R.L. Experiment Station, Wind Mill Creek near telephone line, 2300 ft. alt., E.J.W. (U.S. Forest Service collector) *s.n.*, 15 May 1936 (†MONTU). Gallatin Co.: without definite locality, 5500 ft. alt., *Tweedy* 20 (MONT, NY; †YU p.p., with 1 plant of *T. Hookeri*). **Nebraska.** Brown Co.: Long Pine, *Dudley s.n.*, 7 May 1893 (*ds). Cherry Co.: Valentine, *Bates s.n.*, 15 April 1891 (*NY). Knox Co. (?): Fort Niobrara, *Wilcox s.n.*, May 1888 (*CAN, NY). Lincoln Co.: range south of North Platte, 2900 ft. alt., *Kiener* 18713 (*GH); Hershey, *Mell s.n.*, 20 April 1903 (*us). Red Willow Co.: McCook, *Swezey* (?) 59 (†NY). Sioux Co.: Harrison, *Petersen s.n.*, May 1926 (*NY). Thomas Co.: Halsey, *Mell & Knopf s.n.*, 1 May 1903 (*MO, OC). **Nevada.** Lincoln Co.: hillsides, Pioche, 6000 ft. alt., *McMillan* 436 (*RSA, *UT). **New Mexico.** Bernalillo Co.: Sandia Mts., Albuquerque, 6500 ft. alt., *Brooks* 2819 (*COLO). Colfax Co.: without definite locality, *St. John s.n.*, May 1893 (*GH). Grant Co.: Silver City, *Eastwood* 8187 (*CAS, GH, MO, us). Hidalgo Co.: 1 mi. east of Monument 66, southeast of former site of Cloverdale, *McVaugh & Harvill* 8083 (*MICH). Lincoln Co.: Capitan Mtn., *Huber s.n.*, 28 March 1929 (*PH). Mora Co.: Shoemaker, *Nelson* 168 (*RM); Wagon-mound, *Nelson* 11302 (*RM, UC). Otero Co.: between Mescalero and Cloudcroft, *Wiegand & Wiegand* 2665 (*GH); Guadalupe Mts. near "Box" triangulation station, *Wilkens* 1777 (PH). Quay Co.: Nara Visa, *Fisher* 103 (*us); 15 mi. southwest of Ima, near the Quay-DeBaca county line, *Norvell* 1559 (*ds). San Juan Co.: Aztec, *Baker* 729 (†us p.p., with 6 plants of *T. incana*). San Miguel Co.: hill at railroad station, Las Vegas, *Gray s.n.*, May 1885 (*GH). Sandoval Co. (?): Sandia Mts., mesas and foothills near Madera, *Ellis* 234 (*us). Santa Fé Co.: Chamisa Arroyo, 10 mi. southwest of Santa Fé, *Goodman s.n.*, 23 April 1938 (*NY). Union Co.: just over line from Oklahoma panhandle, *McFarland* 68 (*OKL). **North Dakota.** Billings Co.: Medora, *Moran s.n.*, 22 May 1938 (†OKL). Slope Co.: Bad Lands, Marmarth, *Moyer* 455 (†NY). Stark Co.: prairie, Dickinson, *Reiche s.n.*, 18 May 1942 (†UC). **Oklahoma.** Beaver Co.: 15 mi. southwest of Beaver, *Stevens* 358½ (GH). Blaine Co.: on side of draw leading to the Canadian River, 1 mi. north, 1 mi. east, 2½ mi. north, and 1½ mi. east of Hydro, *Beaman* 689 (CH). Cimarron Co.: top of Black Mesa, Oklahoma-New Mexico state line, 5000 ft. alt., *Goodman* 2419 (OKL). Comanche Co.: Medicine Park, *Myers s.n.*, 20 March 1926 (*CH,

*OKL). Wichita Mts., Hopkins, *Nelson & Nelson* 979 (*RM). Custer Co.: hillside in prairie, 3 mi. south and 7 mi. west of Clinton on Highway 66, *Waterfall* 2554 (CH, *OKL). Greer Co.: 7 mi. southwest of Jester, *Bull* 70 (*OKL). Harper Co.: hills 10 mi. south of Buffalo, *Goodman* 2391 (*OKL); near Buffalo, *Stevens* 307½ (*CH). Roger Mills Co.: Red Lands, *Engleman* 1681 (OKL). Woods Co.: hillside near Alva, *Stevens* 216 (ds, CH, ILL, MO, NY, OKL, *us). Woodward Co.: vicinity of Camp Supply, *Wilcox* s.n., 5 April 1905 (CAN, F, CH, MO, NY, PH, *UC). **South Dakota.** Fall River Co.: slopes just north of Hot Springs, *McIntosh* 672 (†RM p.p., with 2 plants of *T. Hookeri*). Pennington Co.: prairie near Rapid City, *Lee* 529 (*RM). Washabaugh Co.: hillsides, Bear Creek, *Over* 2068 (†us). **Texas.** Armstrong Co.: 2 mi. southwest of Triassic Peak, Palo Duro Canyon State Park, 3400 ft. alt., *Jespersen & Jespersen* 2653 (ds, *uc). Bell Co.: Camp Hood, *Bergseng* s.n., 5 March 1945 (†wis). Brewster Co.: south slopes of hills in Paradise Canyon, 5 mi. west of Alpine, *Brown* B164 (*SRSC); main canyon east of Mt. Ord, Sierra del Norte, about 10 mi. southeast of Alpine, ca. 800 m. alt., *McVaugh & Harvill* 7861 (ds, MICH, NA, *SRSC). Culberson Co.: summits of Guadalupe Mts. above Frijole, 2400 m. alt., *McVaugh & Harvill* 8155 (ds, *CH, MICH, NA, SRSC). Dickens Co.: hills in southeastern part of county, *Engleman* s.n., 20 May 1940 (OKL). El Paso Co.: Hueco Mts., *Thurber* 141 (*CH). Hood Co. (?): bluffs, Falls Creek, *Reverchon* 1533 (ds, F, MO, us). Jeff Davis Co.: Davis Mts., *Allen* s.n., 14 March 1915 (MICH, †NY); hills near Limpia Creek, Davis Mts., *Allen* s.n., 14 March 1915 (*MO); Davis Mts., HO Canyon, near Sawtooth Mtn., ca. 1900 m. alt., *Hinkley* s.n., 13 March 1937 (*CH). Johnson Co.: 15 mi. southwest of Cleburne, *Cory* 53967 (*ws). Lubbock Co.: Bolls Ranch, 10 mi. southeast of Lubbock, *Demaree* 7442 (*ds). Presidio Co.: Gage estate, 7 mi. west of Alpine, *Buechner* s.n., 12 March 1947 (*SRSC). Randall Co.: Palo Duro Canyon, *Glassman* 2280 (*OKL). Terry Co.: Brownfield, *Wooten* s.n., 20 May 1925 (us). **Utah.** Garfield Co.: Bryce Canyon, *Eastwood & Howell* 769-1 (†CAS); Bryce Canyon, 6000 ft. alt., *Stone* 256 (†NY). Salt Lake Co.: Salt Lake City (this locality incorrect?) *Fletcher* s.n., 1911 (†CH). **Wyoming.** Crook Co.: 1 mi west of Hulett, 4000 ft. alt., *Ownbey* 534 (COLO, CH, IDS, MONTU, NY, UC, †UTC, ws). Laramie Co.: Cheyenne, *Nelson* s.n., June 1904 (*RM).

Some difficulty is met with in an attempt to make entirely certain what material is the type of *T. exscapa*. The problem becomes apparent from study of the "type sheet" in Kew (Plate XVII). The plants on this sheet have no label which identifies their locality or collector except the words "Carleton House Drummond," in Hooker's handwriting (*fide* Dr. Rollins). This note at about the middle of the sheet was originally (before the paper was cut and the specimen removed) between two plants of *T. Hookeri* and two more were above this position on the sheet.



MAP 12. Geographic distribution of sexual and apomictic *Townsendia exscapa*.

One plant of *T. exscapa*, now cut out and removed (photographs of the two presently missing plants, the cutouts of which fit into the holes on this sheet, may be seen in Larsen's (1927) revision of *Townsendia* in Plate 7, figs. 29 and 32), was directly below the

note and two more are to the lower left of the sheet. Another plant of *T. Hookeri* is near the lower right of the sheet. A faint pencil line on the sheet divides the last five-mentioned plants from "Carleton House Drummond" and the top four plants of *T. Hookeri*. Recently (at the time of or subsequent to Larsen's study) the plants of *T. exscapa* on the sheet have been marked "1" and the note "1. Aster ? exscapus Richardson Type." has been placed near the bottom of the sheet. The plants of *T. Hookeri* are similarly marked "2" and in the upper left portion of the sheet identified with the note "2. *Townsendia sericea* Hook. Type." These notes were probably added under Larsen's direction or on the basis of her paper (1927) by Dr. A. W. Hill or Mr. T. A. Sprague of Kew. These are the two members of Kew given acknowledgment by Larsen for assistance.

The type-locality of *Aster ? exscapus* (*Townsendia exscapa*) is "at Carleton House" (Richardson, 1823). Three recent collections of *T. exscapa* have been made near Carleton, Saskatchewan (*Frankton* 1132 and 1300, and *Fraser* s.n., 24 May 1938). No specimens of *T. Hookeri* are known from closer than about 240 miles (to the southwest) from Carleton. The plants of *T. exscapa* on the type sheet in Kew are very similar to those of *Frankton* 1300. Thus it seems probable that the plants of *T. exscapa* on this sheet were collected by Richardson at Carleton House. The plants marked "1" on the type sheet are therefore interpreted as the type of *Townsendia exscapa* (Richards.) Porter. After examining a photograph of this sheet, Dr. A. E. Porsild, whose experience with the collections of Richardson and Drummond is well known, has informed me (personal correspondence) that the interpretation outlined above is the most probable one.

Townsendia exscapa has the widest range and is the most polymorphic of the species of *Townsendia*. Its degree of diversity approaches that of the combined diversity of many of the other species of the genus. Although the form of *T. exscapa* sometimes strongly resembles that of *T. leptotes* and *T. Hookeri* in certain areas of its range, it is not closely related to these species. Its ancestral stock appears to have become separated from that of the other two at a relatively early time.

The geographic position of the range of *T. exscapa* is peculiarly and uniquely situated relative to the ranges of the other species of *Townsendia*. If one considers only the sexual plants of this species, then *T. exscapa* ranges mainly to the south and east of the other members of the genus. Also, it occurs at rather low elevations, and there are extensive and nearly contiguous areas

both lower and higher than those presently inhabited by the species. Thus, it probably has not had its range fragmented by climatic fluctuations (as may have happened to some of the more northern and higher elevation species). Rather, as a result of climatic changes, it probably has merely migrated to higher or lower elevations as a single interbreeding population. Consequently, it has undergone only regional differentiation, and no populations have had sufficient geographic isolation to permit the fixation of specific or even varietal distinctions.

In spite of its considerable polymorphy, sexual *T. exscapa* usually is not difficult to determine. The only perplexing specimens from sexual populations are from Chaffee, Lake, and Park counties in Colorado. Superficially these plants resemble *T. Hookeri*. Their actual morphological variation, however, is in the direction of *T. leptotes*. Their leaves are relatively short and narrow and their pubescence is light; the heads are small and the phyllaries narrow. In spite of their deviation away from *T. exscapa*, however, the basic affinity of these specimens seems to be with that species. Only one specimen, *Schedin & Schedin* 478 (near Leadville, Colorado), seems almost wholly intermediate. I have referred it to *T. leptotes*. Field studies near Leadville are needed to amplify the understanding of *T. exscapa* and *T. leptotes* in that area.

Leadville is not the only area where *T. exscapa* and *T. leptotes* present a problem. West of the continental divide in Colorado, apomixis and hybridization apparently are coupled. Some apomictic collections, such as *Baker* 730 and *Pease s.n.*, 16 May 1878, are fairly typical *T. exscapa*. Others, such as *Eastwood* 5259, *Langenheim* 1227, and *Osterhout* 4704, vary strongly toward *T. leptotes*. Nearly linear, involute, lightly pubescent leaves and narrowly lanceolate phyllaries are found in plants which otherwise have the characteristics of *T. exscapa*.

Except in the extreme southwest corner, sexual *T. exscapa* is not known from western Colorado. Apomictic material of this species is fairly widespread in that part of the state. Possibly certain "cold-climate" adaptations of *T. leptotes* have been fixed in *T. exscapa* by apomixis. The occurrence of the latter species over western Colorado may be a result of this fixation.

Sexual populations of *T. leptotes* in southwestern Colorado vary toward *T. exscapa*. This variation, which probably has resulted from hybridization, is considered in the discussion of the former species. Similarly, putative hybridization of *T. exscapa* and *T. Hookeri* is considered in the discussion of the latter.

12. *Townsendia Parryi* D. C. Eat. in Parry

Townsendia Parryi D. C. Eat. in Parry, Am. Nat. 8: 212. 1874.
Type: *Parry 144*, Wind River Mts., Wyoming, 9000 ft. alt., July 1873
([yu ?, holotype, missing] GH, MO, NY, isotypes).

Townsendia Parryi var. *alpina* A. Gray, Proc. Am. Acad. 16: 83. 1880. *Townsendia alpina* (A. Gray) Rydb. Mem. N. Y. Bot. Gard. 1: 390. 1900. Type: *Parry 145*, high divide between Stinking Water and the Yellowstone, Wyoming, 1873 (†CH, holotype; F, MO, NY, isotypes).

Erect, taprooted biennial, or, infrequently, short-lived perennial; mostly few-stemmed, sometimes single-stemmed or rarely abundantly branched; branches from the base, if also from above, late and weak; stems up to 3.5 dm. high, striate, scape-like, usually conspicuously expanded at junction with the head, lightly to heavily pubescent with pilose-strigose, several-celled trichomes; basal leaves spatulate, entire or 3-toothed near the apex, apiculate or mucronate, 1-nerved, thickish, dark green and shiny, nearly glabrous or pubescent along the veins or moderately strigose on both surfaces, up to 10 cm. long and 1.3 cm. wide; upper caudine leaves much reduced, becoming bract-like near the head, with partly scarious margins; heads large, the first-formed one usually conspicuously the largest; involucres up to 4 cm. wide and 1.8 cm. high; phyllaries in 4-7, mostly 5, series, lanceolate, acuminate or rarely acute, with broad, lacerate-ciliate, scarious margins, 4-16 mm. long, 0.8-3 mm. wide, the next-to-inner series usually longest, usually only the outer 2-3 series lightly strigose; ray-florets 20-70, mostly ca. 40; ray-corollas blue or very rarely white or pink, 12-25 mm. long, 2-4 mm. wide; disk-corollas yellow, 4.0-6.0 mm. long; achenes oblanceolate to narrowly obovate, compressed, 2-3-ribbed, with a longitudinal ridge frequently produced on one or both faces of the achene from growth pressure of the imbricate achenes against each other, rather densely pubescent with duplex, evenly or unevenly bifurcate hairs, papillose, 3.2-4.7 mm. long, 1.0-2.2 mm. wide; pappus of the ray- and disk-florets nearly equal, of ca. 15-40 plurisetose, barbellate bristles, 4-7.5 mm. long, slightly exceeding the length of the disk-corollas. $2n = 18$ in sexual plants and $2n = 36$ in apomictic plants. Reproduction predominantly apomictic, sexual only in a small area in northwestern Wyoming and adjacent Montana. Southwestern Alberta and adjacent British Columbia south to central Idaho and northwestern Wyoming. Map 11. Plate XXI, fig. 2.

Representative specimens: CANADA. Alberta. River bar near Waterton townsite, 4100 ft. alt., *Breitung* 15647 (†NY); Morley District, mountainside, Dada (Dead?) mans Gulch, near Seecbee, 6200 ft. alt., *Brinkman* 3554 (†US); Milk River, *Dawson* 7707 (†CAN); head of High River, Rocky Mts., *Craig* 7708 (†CAN); 5 mi. west of Pincher Creek, *Moss* 804 (†DAO, GH, WIS); alpine slopes, Upper Red Deer River, east of Scalp Creek, 7200-7600 ft. alt., *Porsild* 18325 (†CAN, GH). British Columbia. Crow's Nest Pass, 6000 ft. alt., *Henry* 7 (†CH). UNITED STATES. Idaho. Clark Co.: above basin at head of Webber Creek, west of Argora, 10,000 ft. alt., *Cronquist* 1979 (MO, †UTC). Custer Co.: 8 mi. northeast of Dickey, at Double Springs sum-

mit, on ridge rising north of pass, *Christ & Christ* 17777 (\dagger NY); on upper slopes of Mt. Borah, Chilly, *Christ & Ward* 10442 (\dagger NY); hillside in Willow Creek Canyon, 8 mi. northeast of Dickey, 8000 ft. alt., *Cronquist* 3151 (CH, \dagger DS, MO); Railroad Ridge, 9500 ft. alt., *Davis* 629 (CAS, \dagger DS, MO, WS); mtn. tops near Challis, 8000 ft. alt., *Henderson* 3680 (\dagger US); meadow over ridge west of head of Mahogany Creek, Lost River Mts., vicinity of Mt. Borah, *Hitchcock & Muhlick* 11046 (CAN, CAS, DS, F, CH, \dagger DS, MO, NY, PH, RM, UC, US, UTC, WS, WTU); 7 mi. north of Dickey, Highway 93, *Preece & Turner* 2412 (\dagger WS). Fremont Co.: Henry Lake, 6000 ft. alt., *Payson & Payson* 2026 (CAS, CM, MO, \dagger CH, NY, RM). Lemhi Co.: 9 mi. east of Leadore, *Christ & Ward* 14823 (\dagger NY); Liberty Mtn., in Lemhi Range west of Gilmore, *Christ & Ward* 14872 (NY); ca. 4 mi. south of Lemhi, *Hitchcock & Muhlick* 9223 (\dagger WTU); knoll near head of Spring Canyon ca. 8 mi. southeast of Gilmore, Lemhi Mts., *Hitchcock & Muhlick* 9318 (CAS, NY, UC, UTC, \dagger WS, WTU). Montana. Beaverhead Co.: slopes 10 mi. east of Monida, *Nelson & Nelson* 5425 (CM, \dagger DS, GH, MO, NY, POM, RM, UC, US, WS, WTU). Broadwater Co.: summit of grade between Townsend and White Sulphur Springs, *Hitchcock & Muhlick* 11858 (CAN, CAS, DS, GH, MO, PH, RM, *UC, UTC, WS, WTU). Carbon Co.: meadow 17 mi. southwest of Red Lodge, Beartooth Mts., 8500 ft. alt., *Rollins & Muñoz* 2825 (DS, GH, \dagger US). Fergus Co.: meadow on high plateau to east of Half Moon Canyon, Big Snowy Mts., *Hitchcock & Muhlick* 11918 (CAN, CAS, DS, GH, MO, MONT, PH, RM, UC, UTC, \dagger WS, WTU). Gallatin Co.: Valley View, 1 mi. southwest of Bozeman, *Booth* 1512 (*MONT, MONTU, UTC, WS, WTU); above timberline on Mt. Baldy, near Bozeman, 8500 ft. alt., *Brown* 551 (*MICH); Bridger Mts., 7000 ft. alt., *Rydberg & Bessey* 5132 (CAN, F, GH, MONT, *MONTU, NY, PH, RM, US). Glacier Co.: bluffs, Midvale, *Umbach* 254 (COLO, \dagger DS, F, MSC, RM, US, WS). Lewis and Clark Co.: high cliffs directly south of Gibson Lake, and ca. 3 mi. southwest of Gibson Dam, ca. 25 mi. northwest of Augusta, Lewis and Clark National Forest, *Hitchcock* 18041 (\dagger RM, RSA, UC, WS, WTU). Liberty Co.: Cottonwood Coulee, 20 mi. south of Chester, *Marks s.n.*, 10 July 1946 (\dagger WS). Madison Co.: $\frac{1}{2}$ mile north of Kock Peak, Taylor Mts., *Hitchcock & Muhlick* 15170 (DS, MO, RM, \dagger RSA, UC, WS). Meagher Co.: along Checkerboard Creek, northeast base of Castle Mts., *Hitchcock & Muhlick* 12152 (CAN, CAS, DS, GH, MO, PH, *RM, UC, UTC, WS, *WTU); southwest slope of King's Hill, Little Belt Mts., 7900 ft. alt., *Hitchcock & Muhlick* 12340 (PH, WS, \dagger WTU). Park Co.: Gardiner, *Hawkins* 197-i (\dagger MONT); Cooke Guard Station, near Cooke City, *Ownbey s.n.*, 1948 (\dagger WS); near top of hills along Yellowstone River, 19 mi. northeast of Livingston (just south of Springdale), *Ownbey* 3369 (*WS); meadows, Cooke Guard Station, 3 mi. east of Cooke City, 8000 ft. alt., *Witt* 1162 (RSA, \dagger WS, WTU). Powell Co.: benches bordering Blackfoot River ca. 16 mi. west of Lincoln on Ovando Road, *Hitchcock & Muhlick* 11578 (CAN, CAS, DS, CH, ILL, MO, MONT, PH, RM, UC, US, UTC, \dagger WS, WTU).

Silver Bow Co.: hills, Melrose, *Shear* s.n., 5 July 1895 (†NY). Stillwater Co.: bluff south of Yellowstone River, 30 mi. southeast of Big Timber (east of Reedpoint), *Ownbey* 3371 (*ws). Sweetgrass Co.: Wreck Creek, Greycliff, 1200 m. alt., *Eggleson* 7883 (*NY, us). Wheatland Co.: bench near Big Elk Creek, southwestern part of county, *Hitchcock* 2360 (CAS, *MONTU, POM). Oregon. Wallowa Co.: ridges of the Wallowa Mts., 7000 ft. alt., *Cusick* 2295 (F, GH, †MO, MSC, ND, RM, UC, US, ws). Wyoming. Big Horn Co.: near Medicine Mtn., 8000 ft. alt., *Williams & Williams* 3035 (GH, MO, NY, RM, †ws, WTU). Fremont Co.: low hilltop, Dickenson Park, Wind River Mts., *Rollins & Costello* 2048 (†GH, MO). Lincoln Co.: ridge near Cottonwood Lake, east of Smoot, 10,300 ft. alt., *Payson & Armstrong* 3693 (COLO, GH, ILL, †MO, MSC, PH, POM, RM). Park Co.: meadow, summit of Clay Butte, west of Beartooth Butte, 10,000 ft. alt., *Porter* 5881 (COLO, DAO, DS, GH, PH, RM, †RSA, UC, WTU). Sheridan Co.: knoll at top of Red Grade, west of Big Horn, Big Horn Mts., *Rollins* 511 (†DS). Sublette Co.: Wyoming Range, 15 mi. west of Merna, *Payson & Payson* 2762 (F, GH, MO, PH, POM, RM, †UC, US). Teton Co.: south slope of Sheep Mtn., 9000 ft. alt., *Murie* 2828 (†NA). Washakie Co.: upper Ten Sleep Canyon, ca. 7500 ft. alt., *Ownbey* 805 (RM, †ws). Yellowstone National Park: hills near Mammoth Hot Springs, 6000 ft. alt., *Burglehaus* s.n., July 1893 (ILL, MICH, †MO, MSC, NY, OC, POM, US, UT, WTU); hillside, Mammoth, *Davis* 5332 (†DS, UC); Mammoth Hot Springs, *Tweedy* 158 (NY, *YU).

Townsendia Parryi is a relatively unspecialized member of the genus and is most closely related to several morphologically more advanced species. Its relatives mostly occupy more arid habitats than does *T. Parryi*. The clearly marked features of this species are blurred only by hybridization with *T. florifer*. The putative hybrids occur in collections from apomictic populations.

The ranges of *T. florifer* and sexual *T. Parryi* do not overlap. They most closely adjoin in the corners of northeastern Idaho and northwestern Wyoming. Some of the intermediate plants are found in that area. In addition, a single sexual collection (*Tweedy* 158) of *T. Parryi* which shows faintly the influence of *T. florifer* is also from this area (Yellowstone National Park). In Idaho the probable hybrids are in an area of overlap of the ranges of *T. florifer* and apomictic *T. Parryi* in Custer County. The characters of pure *T. Parryi* and pure *T. florifer* and their putative hybrids are compared in tabular form below.

The following collections are putative apomictic hybrids of *T. florifer* and *T. Parryi*: *Burglehaus* s.n., July 1893 (MICH, MO, NY, POM, US, UT, [WTU is a non-hybrid apomict]); *Christ & Christ* 17777 (NY, p.p., with non-hybrid apomicts); *Christ & Ward* 14823 (NY); *Cronquist* 3151 (GH, IDS, MO, ws); *Hawkins* 197-i (MONT);

<i>T. Parryi</i>	<i>T. florifer</i>	<i>putative hybrids</i>
Plants few-stemmed.	Plants many-stemmed.	Plants few- to many-stemmed.
Stems, at least the first-formed ones, thick.	Stems slender.	Stems slender.
Phyllaries acuminate, mostly in 5-7 series.	Phyllaries acute, in 2-4 series.	Phyllaries acute or acuminate, mostly in 5-6 series.
Ray-corollas blue, glabrous.	Ray-corollas whitish-pink, glandular (in the area of the hybrids).	Ray-corollas mostly blue (difficult to determine from herbarium material), glandular.

Henderson 3680 (us); *Hitchcock & Muhlick* 9223 (wru); *Preece & Turner* 2412 (ws). *Burglehaus* s.n., *Hawkins* 197-i, and *Henderson* 3680 are strongly intermediate types, while the others are closer to pure *T. Parryi*. The fact that these obligate apomicts are not all intermediate between *T. Parryi* and *T. florifer* in the same degree suggests that more than one change from sexuality to apomixis after hybridization may have occurred.

The apomorphic material (*Parry* 145) described by Gray as *T. Parryi* var. *alpina* also appears to be of hybrid derivation. These plants have pink, glandular ray-corollas and abundant pubescence of long trichomes. The presence of these characters suggests that hybridization has occurred between *T. condensata* and *T. Parryi*. *Parry* 145 was collected near the eastern boundary of Yellowstone National Park where the ranges of sexual *T. condensata* and sexual *T. Parryi* most closely approach each other. It should be noted that Larsen (1927) placed *T. Parryi* var. *alpina* in synonymy under *T. spathulata*. It is not that species. On two sheets which Larsen examined (MO, PH) it was accompanied by plants of *Parry* 142 (*T. spathulata*). The superficial resemblance of these may have caused her misdetermination.

The abundance of apomixis in this primarily biennial species is surprising, but the distribution pattern of the apomorphic types is not unusual. The success of the apomicts in populating higher elevations and higher latitudes not occupied by the sexual forms is evident in their geographic distribution (Map 11). However, it is peculiar that apomixis is nearly absent within the range of the sexual types. Within this area a sexual form (*Brown* 551) has been found even above timberline.

13. *Townsендia florifer* (Hook.) A. Gray

Townsендia florifer (Hook.) A. Gray, Proc. Am. Acad. 16: 84. 1880. *Erigeron*? *florifer* Hook. Fl. Bor.-Am. 2: 20. 1834. *Aplopappus*

florifer (Hook.) Hook. & Arn. Bot. Beechey Voy. 351. 1840. *Stenotus florifer* (Hook.) T. & G. Fl. N. Am. 2: 238. 1842. Type: *Douglas s.n.*, Priest's Rapids of the Columbia (k, examined by Dr. R. C. Rollins).

Townsendia Watsoni A. Gray, op. cit. p. 84. *T. florifer* (Hook.) A. Gray var. *Watsoni* (A. Gray) Cronquist, Leafl. West. Bot. 6: 49. 1950. Type: *Watson* 520, Stansbury Island, Tooele Co., Utah (GH, holotype; us, YU, isotypes).

Townsendia scapigera D. C. Eat. in S. Wats. var. *ambigua* A. Gray, op. cit. p. 84. *T. ambigua* (A. Gray) Rydb. Fl. Rocky Mts. 874, 1067. 1917. Type: *Ward* 523, Rabbit Valley, Wayne Co., Utah, 6800 ft. alt. (CH, holotype; us, isotype).

Townsendia florifer (Hook.) A. Gray var. *communis* M. E. Jones, Proc. Cal. Acad. Sci. 5: 697. 1895. Original material: *Jones* 5315b, 10 mi. south of Coyote, Garfield Co., Utah, 6500 ft. alt. (us); *Jones* 5322f, Kingston, Piute Co., Utah, 5300 ft. alt. (POM, us); *Jones* 5323, Marysville, Piute Co., Utah, 6000 ft. alt. (F, MO, MSC, POM, us).

Caulescent, taprooted, winter annual or biennial; stems ascending-suberect, branched at the base and sometimes above, strigose-hirsute, up to 2.5 dm. high; basal leaves spatulate or infrequently oblanceolate, entire, obtuse or acute, sometimes mucronate, strigose, up to 60 mm. long and 12 mm. wide; caudine leaves oblanceolate, spatulate, or linear, strigose, up to 40 mm. long, 1.8-8 mm. wide; heads terminating the stems; involucres campanulate, 15-35 mm. wide (sometimes narrower in late-formed heads), 6.5-14 mm. high; phyllaries in 3-4 (rarely 2) series, pliant in texture, lanceolate, acute, with ciliate or lacerate-ciliate, scarious margins, strigose on the outer surface, 4-12 mm. long, 1-3 mm. wide; ray-florets ca. 15-30; ray-corollas white to pinkish, usually darker abaxially, frequently glandular on the abaxial surface (rarely also glandular on the adaxial surface), 8-16 mm. long, 1.5-2.5 mm. wide; disk-corollas yellow, frequently tipped or tinged with pink, 3.3-6.3 mm. long; achenes oblanceolate to narrowly obovate, compressed, 2-ribbed, those of the ray-florets rarely 3-ribbed, pubescent with duplex, bifurcate or unequally forked hairs with the prongs not recurved, papillose, 3.5-5.6 mm. long, 1.1-2.1 mm. wide; disk-pappus of ca. 20-40 plurisetose, obcompressed, barbellate or ciliate bristles, 3.5-7.6 mm. long, usually slightly exceeding the length of the disk-corollas; ray-pappus of ca. 20-30 bristles, similar to but shorter than those of the disk-pappus, 2-6.7 mm. long, or of short bristles or squamellae less than 2 mm. long. $2n = 18$. Reproduction sexual. Eastern Idaho to central Washington and south to southern Oregon, northeastern Nevada, and southern Utah. Map 13. Plate XXI, fig. 3.

Representative specimens. Idaho. Bannock Co.: Pocatello, *Henderson* 4105 (cs, CH, RM). Bingham Co.: Blackfoot, *Moore* (?) s.n., 28 May 1904 (CH). Bonneville Co.: Idaho Falls, *Ayres* 4460 (NY). Butte Co.: Arco, 5300 ft. alt., *Macbride & Payson* 3095 (CM, CH, MO, NY, RM, us). Canyon Co.: Lowell Butte, near Caldwell, *Cronquist* 103-36 (UTC); near Nampa, *Mulford* s.n., 1 July 1892 (CH, MO, *NY). Clark Co.: Paddock No. 1, U. S. Sheep Experiment Station, S. 27, T. 11 N., R. 36 E., *Lingenfelter* 541 (*NY, RSA, WS, WTU). Custer Co.: near Willow Creek, 4 mi. northeast of Dickey, 7000 ft. alt., *Cronquist*

3147 (GH, MO); ca. 15 mi. west of MacKay, *Hitchcock & Muhlick* 8901 (CAN, CAS, DS, GH, *NY, RM, UC, UTC, WS, WTU); Custer-Lemhi Co. line, Highway 93, *Preece & Turner* 2389 (*ws). Elmore Co.: King Hill, 2580 ft. alt., *Nelson & Macbride* 1129 (CAN, DS, F, GH, MO, MONT, *NY, POM, RM, UC, us). Fremont Co.: hills near St. Anthony, *Quayle* 41 (DS, POM, RM, UC). Gooding Co.: 8 mi. south of Gooding, *Christ & Ward* 7190 (NY). Jefferson Co.: 10 mi. northwest of Terreton, *Christ* 12275 (*NY). Lemhi Co.: 25 mi. southwest of Salmon, *Christ* 12231 (NY); Birch Creek, R29E, T11N, *Davis* 3800 (IDS, *NA, UC, ws). Lincoln Co.: Shoshone, *Palmer* 562 (us). Minidoka Co.: 7 mi. southeast of Minidoka, *Christ & Ward* 7896 (NY). Oneida Co.: 7 mi. west of Holbrook, *Christ* 12320 (NY). Owyhee Co.: 3 mi. north of Murphy, *Christ* 9563 (NY); Bruneau, *Jones* s.n., 23 June 1930 (DS, *MO, MONTU, POM, WTU); Reynolds Creek, 5000 ft. alt., *Macbride* 1017 (DS, GH, MO, RM); ½ mi. southeast of Grand View, *Maguire & Holmgren* 26214 (CAN, CAS, COLO, DS, IDS, MO, NY, PH, POM, UC, US, UTC, WS, WTU). Payette Co.: New Plymouth, 2200 ft. alt., *Macbride* 90 (CM, DS, GH, ILL, MO, NY, RM, UC, US, ws). Twin Falls Co.: Twin Falls, *Bennett* 75 (RM). Nevada. Elko Co.: highway 40, 2 mi. west of Wendover, *Cantelow* s.n., 10 May 1942 (cas); vic. Furguson Springs, 4500 ft. alt., *Holmgren & Lund* 3 (UTC); 20 mi. west of Goldhill, Utah, 4900 ft. alt., *Maguire & Becroft* 2828 (UTC); Silver Zone Pass, 5200 ft. alt., *Ripley & Barneby* 4613 (cas). White Pine Co.: 8 mi. west of Baker, 5800-6100 ft. alt., *Ripley & Barneby* 3569 (cas). Oregon. Baker Co.: Huntington, *Sweetser* (?) s.n., (UC). Crook Co.: just west of Prineville, Twp. 14 S., R. 15 E., S. 36, 2900 ft. alt., *Cronquist* 6960 (*GH, ws); Cline Falls, *Nelson* 815 (CM, GH, MO, NY, *RM, UC). Deschutes Co.: 15 mi. north of Bend, ca. 3500 ft. alt., *Hitchcock & Martin* 4906 (DS, NA, *NY, POM, UC, UTC, WS, WTU). Gilliam Co.: west slope along John Day River, 1 mi. above the mouth of Rock Creek, Twp. 1 N., R. 19 E., *Cronquist* 6209 (ws). Harney Co.: western slopes north of Squaw Butte, Squaw Butte Experiment Station, *Maguire & Holmgren* 26510 (NY, UC, UTC). Jefferson Co.: flats at Cove Palisades, 13 mi. southwest of Madras, Twp. 12 S., R. 12 E., S. 2., 1900 ft. alt., *Cronquist* 6946 (CAS, DS, ILL, RSA, UC, UTC, WS). Lake Co.: hills west of Silver Creek, *Cusick* 2616 (F, GH, MO, MSC, ND, *NY, POM, RM, UC, US, ws). Malheur Co.: near Vale, *Leiberg* 2067 (GH, MO, NY, PH, UC, US). Morrow Co.: slopes about 10 mi. north of Lexington, Twp. 1 N., R. 26 E., *Cronquist* 6593 (WS, WTU); near Lexington, 420 m. alt., *Leiberg* 34 (F, GH, *MO, NY, POM, UC, us). Umatilla Co.: about 20 mi. south of Umatilla, just east of Butter Creek, Twp. 2 N., R. 27 E., *Cronquist* 6589 (COLO, DAO, OKL, RSA, UTC, WS, WTU). Wasco Co.: near Shaniko, *Gale* 101 (MO, PH). Utah. Beaver Co.: Frisco Mine, on Highway 21, ca. 30 mi. west of Milford, 5000 ft. alt., *Cottam* 4636 (UC); Milford, *Goodding* 1046 (GH, RM). Box Elder Co.: 20 mi. north of Lucien, *Maguire & Maguire* 21518 (CAN, GH, *MO, NY, PH, UTC, WS, WTU). Garfield Co.: 10 mi. south of Coyote, 6500 ft. alt., *Jones*

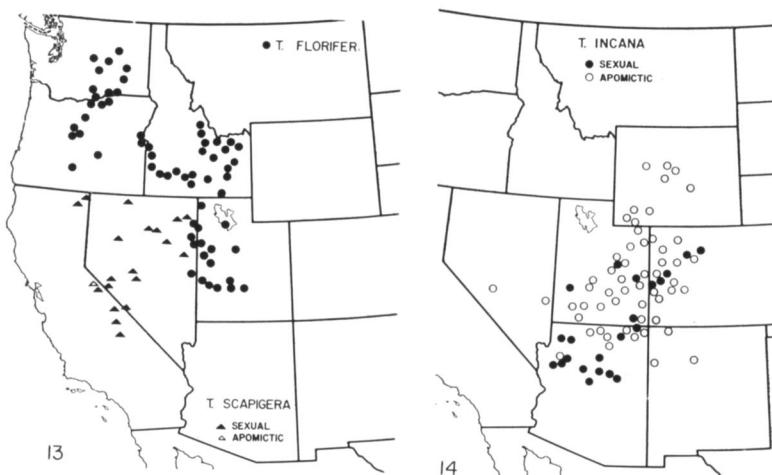
5315b (us). Juab Co.: 2 mi. east of Troutcreek, 5000 ft. alt., *Maguire & Becroft* 2829 (GH, UTC). Millard Co.: 37 mi. west of Delta, 5200 ft. alt., *Maguire & Becroft* 2830 (POM, *RM, UC, UTC); Warm Point Ridge, west end Pine Valley, 5 mi. west Hdqts. Desert Range Experiment Station, *Maguire* 20880 (CH, *NY, UTC). Piute Co.: Marysvale, 6000 ft. alt., *Jones* 5323 (F, MO, MSC, POM, US). Sevier Co.: Joseph City, 5500 ft. alt., *Jones* 6379 (*MO, POM, US). Tooele Co.: Gold Hill, *Jones* s.n., 6 June 1917 (POM); Dugway, *Jones* s.n., 30 May 1891 (cs, GH, POM); Stansbury Island, *Watson* 520 (GH, US, YU). Tooele or Utah Co.: Mercur, 5500 ft. alt., *Jones* s.n., 6 June 1896 (POM). Utah Co.: Goshen, *Garrett* 3955 (UT). Wayne Co.: Rabbit Valley, 6800 ft. alt., *Ward* 523 (GH, US). Washington. Adams Co.: Ritzville, 488 m. alt., *Sandberg & Leiberg* 169 (CAN, CAS, F, GH, MO, NY, PH, UC, US, WS). Benton Co.: Columbia River opposite Umatilla, *Howell* s.n., 29 April 1882 (CAN, CM, F, MO, PH, US). Chelan Co.: slopes near Wenatchee, *Cantelow* s.n., (WTU). Franklin Co.: hillside, Kahlotus, *Cotton* 1013 (US, WS). Grant Co.: slopes north of Soap Lake in Grand Coulee, *Thompson* 11498 (CAS, DAO, DS, *GH, MO, MONT, MONTU, NA, NY, PH, POM, RSA, US, WS, WTU). Kittitas Co.: near Vantage, *Thompson* 13707 (F, GH, MO, NY, US). Klickitat Co.: Columbia River opposite Willows, *Howell* s.n., 18 April 1880 (CH). Lincoln Co.: slopes at Almira, *Thompson* 11666 (CAS, DS, MO, NY, POM, WTU). Walla Walla Co.: hills, Wallula, *Cotton* 1034 (US, WS). Yakima Co.: ravine near Highway 97, on Logy Creek, *Hitchcock & Martin* 3386 (DS, NA, POM, RM, RSA, UC, WS, WTU).

Townsendia florifer is a sharply defined species and may be determined with ease. It has been taxonomically troublesome, however, when attempts have been made to distinguish *T. Watsoni* A. Gray from *T. florifer*. The type of *T. Watsoni* (*Watson* 520) is from near the center of the geographic range of *T. florifer* and is intermediate in the gamut of morphological variation of *T. florifer*. It cannot, therefore, be maintained at the specific or varietal level.

Townsendia florifer is closely related to *T. Parryi*. The two species occasionally have been confused, apparently because of hybridization between them. This is considered in the discussion of *T. Parryi*. The close phylogenetic relationship of *T. florifer* and *T. scapigera* is considered in the discussion of the latter species.

Townsendia florifer is common and has been abundantly collected along the Snake River Plains of Idaho and in central Oregon and western Utah. It flowers mostly in May and June. Between Hinkley, Utah and the Utah-Nevada boundary, I made arbitrary stops every 10 miles for 70 miles, during the summer of 1954. A plant or two of *T. florifer* was found at three of these stops. At two non-arbitrary stops plants were also found. It

appears that the species is ubiquitous in that area. It probably is abundant only in moist seasons.



MAPS 13-14. 13. Geographic distribution of *Townsendia florifer* and sexual and apomictic *T. scapigera*. 14. Geographic distribution of sexual and apomictic *T. incana*.

14. *Townsendia scapigera* D. C. Eat. in S. Wats.

Townsendia scapigera D. C. Eat. in S. Wats. Bot. Expl. Fortieth Parallel, 145, pl. 17. 1871. Type: Watson 518, Trinity Mts., 5000 ft. alt., Pershing Co., Nevada, May 1868 (yu, holotype; us, isotype).

Townsendia scapigera var. *caulescens* D. C. Eat. in S. Wats. ibid. p. 145. Type: Watson 519, Monitor Valley, 5000 ft. alt., Nye Co., Nevada (yu, holotype; GH, NY, US, isotypes).

Cespitose, taprooted biennial or short-lived perennial; much-branched and densely leafy at the base, sometimes with a well-developed woody caudex with prominent leaf scars; leaves spatulate, entire, obtuse, sometimes mucronate, infrequently emarginate, strigose, up to 70 mm. long (averaging ca. 30 mm.) and 9 mm. wide (averaging ca. 5 mm.); peduncles from the ends of the stems, naked or infrequently with 1 or 2 reduced leaves, striate, strigose or pilose, more densely pubescent near the head, slightly expanded near the junction with the head, up to 1.2 dm. long; involucres obconical-campanulate, 12-32 mm. wide, 7-14 mm. high; phyllaries in 3-4 (rarely 5) series, pliant in texture, lanceolate, acute, with lacerate-ciliate, scariosus margins, strigose or pilose-strigose on the outer surface, 3-13 mm. long, 1-2.8 mm. wide; ray-florets ca. 18-35; ray-corollas whitish, pinkish, or dull red, densely glandular on the abaxial surface, 6.5-16 mm. long, 1.5-2.4 mm. wide; disk-corollas yellow, frequently pink-tipped or tinged, 3.6-5.4 mm. long; achenes oblanceolate, compressed, 2-ribbed, those of the ray-florets rarely 3-ribbed, pubescent with long, thin, duplex, bifurcate hairs, papillose,

3.8-5.6 mm. long, 1.1-2.0 mm. wide; pappus of ca. 20-30 plurisetose bristles, the bristles awl-shaped, obcompressed, densely barbellate or ciliate; ray-pappus 3.1-6.2 mm. long, disk-pappus slightly longer than the ray-pappus, 5.0-7.2 mm. long, slightly exceeding the length of the disk-corollas. Reproduction mostly sexual, rarely apomictic. Nevada and eastern California. Map 13. Plate XXI, fig. 4.

Representative specimens. **California.** Inyo Co.: Teufel Canyon, Inyo Mts., 25 mi. northwest of Darwin, 4600 ft. alt., *Jaeger s.n.*, 28 May 1938 (POM); Teufel Canyon, southern Inyo Mts., 5200 ft. alt., *Jaeger s.n.*, 27 May 1939 (ds); Seep Hole Spring, Inyo Mts., *Kerr s.n.*, May 1940 (*CAS); Reed Flat and 1 mi. south of Reed Flat, White Mts., 10,000 ft. alt., *Roos & Roos 5120* (ds, *RSA, UC); Westgard Pass, 7000 ft. alt., *Alexander & Kellogg 2492* (UC, WS); Westgard Pass, summit of ridge above small canyon, 7300 ft. alt., *Alexander & Kellogg 2492a* (ds, UC); Mazourka Canyon, 7800 ft. alt., *Alexander & Kellogg 2993* (MO, *RM, UC, US, UTC); Cerro Gordo Peak, crest of divide above Cerro Gordo Mines, 8000 ft. alt., *Alexander & Kellogg 3020* (UC). Modoc Co.: Ft. Bidwell, *Austin s.n.*, April 1878 (GH); Buffalo Ravine, near Surprise Valley, *Lemmon 29* (*MO, YU); Warner's Ranch, *Lemmon s.n.*, May 1879 (UC). Mono Co.: western side of Sweetwater Canyon, 10,500 ft. alt., *Alexander & Kellogg 3959* (*UC); top of divide east of Deep Creek, 11,200 ft. alt., *Alexander & Kellogg 4053* (GH, MO, RM, *UC, UTC, WTU); divide, 1 mi. north of Mt. Patterson, 11,000 ft. alt., *Alexander & Kellogg 4556* (MO, UC); east of Swamp Meadows, 9500 ft. alt., *Alexander & Kellogg 4561* (GH, *MO, UC, UTC); 15 mi. north of Mono Lake P. O., on Conway Grade (to Bridgeport), ca. 7500 ft. alt., *Blake 11831* (ds). Plumas Co.: without definite locality, *Austin s.n.*, 1880 (NY). **Nevada.** Elko Co.: north of Deeth, upper Humboldt Valley, 5350 ft. alt., *Hall 10365* (*UC); Cobre, 6000 ft. alt., *Jones s.n.*, 16 June 1906 (POM); mesas and hills, near Cave Creek Post Office, Ruby Valley, *Mason 4694* (UC). Esmeralda Co.: between Pinchot Creek and Pinon Hill on road to B. & B. Mine, 6700 ft. alt., *Duran 2758* (*UC); Magruder Mtn. south end of the Silver Peak Range, 8200 ft. alt., *Maguire & Holmgren 25640* (GH, NY, UC, *UTC). Eureka Co.: Palisade, *Jones s.n.*, 14 June 1882 (POM). Humboldt Co.: 5 mi. north of Farnham Hot Springs, Quinn River Valley, 5000 ft. alt., *Train TC4* (US). Lander Co.: Victory Highway, 20 mi. east of Battle Mountain, *Eastwood & Howell 175* (CAS). Mineral Co.: top of ridge, north, overlooking Hawthorne, 9500 ft. alt., *Alexander & Kellogg 4440* (*UC); Mount Grant, Wassuk Range, 10,000 ft. alt., *Archer 7130* (UC); road west to Laphan Canyon rim along north basin, edge of Laphan Meadows, west slope of Mt. Grant, Wassuk Range, 9400 ft. alt., *Train 4178* (RSA, UC). Nye Co.: 4 mi. south of Millett, 5500 ft. alt., *Lindsdale & Linsdale 690* (CAS, UTC); west slope, Toquima Range, mouth of Mariposa Canyon on Manhattan-Round Mountain road, 5700 ft. alt., *Train 2738* (NY, UC, UTC, WTU). Pershing Co.: Rochester,

mtn. slopes, 4000 ft. alt., *Train R30* (us); Trinity Mts., 5500 ft. alt., *Watson 518* (ny); Pah-Ute Mts., 5500 ft. alt., *Watson 518* (ch). White Pine Co.: Warm Springs, *King s.n.*, May 1918 (cas).

Townsendia scapigera is morphologically closest to the central Oregon populations of *T. florifer*. In that area the stem leaves of *T. florifer* are few and the base of the plant is very leafy. Only a slight change from that condition would be required to produce *T. scapigera*. In northeastern Nevada, on the other hand, where the ranges of *T. scapigera* and *T. florifer* most closely adjoin, the two species are more distinct. The stems of *T. florifer* in that area are abundantly leafy upward and not very leafy at the base. This conspicuous difference between *T. scapigera* and *T. florifer* in that area is a further reason for maintaining a specific rather than a varietal distinction between them. More collecting in northern Nevada and southern Oregon will be required to elucidate completely the status of the two species.

Townsendia scapigera attains a considerable degree of diversity in the mountains of Inyo and Mono Counties in California. This diversity has already been noted by Heiser (1948). He suggested that apomixis might be involved. It is involved, but probably is not important in increasing the diversity of these populations. The large plants in the mountains of Mono County probably have become differentiated from the smaller plants in the mountains of Inyo County largely as a result of geographic semi-isolation.

In Inyo County especially, one might expect the development of different ecotypes. In that county, plants have been collected as low as 4600 ft. elev. (*Jaeger s.n.*, 28 May 1938) and as high as 10,000 ft. (*Roos & Roos 5120*). This is the greatest elevational range in a species of *Townsendia*. If ecotypes have developed, they are not very apparent in herbarium material, however. The only obvious feature is that the low-elevation plants are smaller and shorter-lived than those from higher elevations.

Apomixis in this primarily biennial species parallels the correspondingly small amount in another biennial, *T. grandiflora*. Apomixis in these species is rare, and occurs only in plants of high elevations. In the Sweetwater Mountains of California, plants from the summit or very near the summit of the mountains are apomicts. Morphologically very similar sexual plants (*Alexander & Kellogg 4561*) occur on a protected knoll about 1000 ft. below the summit of the mountains. The apomicts must have some adaptational qualities, not present in the sexual plants, which better suit them to the tops of these mountains.

15. *Townsendia condensata* D. C. Eat. in Parry

Townsendia condensata D. C. Eat. in Parry, Am. Nat. 8: [106 nom. nud.] 213. 1874. Type: *Putnam s.n.*, Washakies Needles, Owl Creek Range, Hot Springs Co., Wyoming, 1873 (yu, holotype; †CH, isotype).

Townsendia anomala Heiser, Madroño 9: 240. 1948. Type: *von Schrenk s.n.*, Holm Lodge, about 40 mi. west of Cody, Park Co., Wyoming, 26 Aug. 1922 (MO, holotype).

Rosulate-pulvinate, taprooted, short-lived perennial; caudex becoming moderately branched, sometimes elongate, often subterranean; stems few and very short or sometimes nearly absent in alpine plants, or sometimes numerous and several-branched in lower-elevation plants; leaves spatulate with a short, abruptly expanded blade portion and a longer, narrow, petiole-like portion, obtuse or rarely acute, lightly to very densely villous-woolly with simple, several-celled trichomes with conspicuous end-walls, 12-35 mm. long, 2-4 mm. wide; heads in alpine plants mostly sessile and embedded in the tufts of leaves, in plants of lower elevations the first-formed head usually sessile, the later, lateral heads terminating the stems in a corymbose manner; involucres 10-40 mm. wide, 8-18 mm. high; phyllaries in 3-5 series, lanceolate or sometimes linear, acuminate or less often acute, scarious- and long-ciliate-margined, abundantly pubescent with long, several-celled trichomes with conspicuous end-walls, 4-14 mm. long, 0.5-2.8 mm. wide; ray-florets ca. 12-100; ray-corollas whitish or pink to light lavender, glandular on the abaxial surface, 8-16 mm. long, 1.5-3 mm. wide; disk-corollas yellow, sometimes pink-tinged, 4-6.5 mm. long; achenes oblanceolate, compressed, 2-ribbed, those of the ray florets sometimes 3-ribbed, moderately pubescent with bifurcate or entire, duplex hairs, papillose, 3.2-4.5 mm. long, 0.8-1.3 mm. wide; pappus of the ray- and disk-achenes similar, of ca. 20-35 plurisetose, barbellate bristles, deciduous in a ring around the apex of the achene, 4.4-8.0 mm. long. $2n = 18$ in sexual plants and $2n = 36$? in apomictic plants. Reproduction predominantly apomictic, rarely sexual. Mostly at high elevations, western Montana and Wyoming to east-central California. Map 15. Plate XXIII, figs. 2 and 3.

Representative specimens. **California.** Mono Co.: western side of Sweetwater Canyon, 10,500 ft. alt., Alexander & Kellogg 3953 (†UC); top of divide east of Deep Creek, 11,200 ft. alt., Alexander & Kellogg 4061 (†UC); R. 34 E., T. 5 S., Sec. 2, White Mt. U.S.G.S. Map, 11,500 ft. alt., Duran 1662 (†UC); north slopes of Sheep Mt., White Mts., Maguire & Holmgren 26109 (†UTC). **Idaho.** Custer Co.: saddle near head of Rock Creek, ca. 1 mi. northwest of Mt. Borah, Beaman 893 (†CH); Lost River Mts., 1 mi. west of Borah, at summit of Saddle between Rock and Mahogany Creeks, 10,800 ft. alt., Hitchcock & Muhlick 10977 (CAS, DS, †NY, RM, UC, UTC, WS, WTR). **Montana.** Glacier Co.: Aberkuny [Appekunny Mtn.], Glacier Nat. Park, 8000 ft. alt., Evans s.n., 16-30 July 1924 (†F). Park Co.: Ram Pasture Mtn., on the Wyoming border, northeast of Cooke City, Witt 1884 (†WS). **Wyoming.** Fremont Co. (?): Wind River, Parry 143 (CH). Hot Springs Co.: Washakies Needles, Owl Creek Range,

Putnam s.n., 1873 (\dagger_{CH} , *yu*). Park Co.: south-facing slope near Holm Lodge on Crossed-Sabre Ranch, 8 mi. east of the east entrance of Yellowstone National Park, 7000 ft. alt., *Beaman & Preece* 503 (CH , **ws*); Holm Lodge, about 40 mi. west of Cody, *von Schrenk s.n.*, 26 Aug. 1922 (*MO*).

This species has long been problematical to the few botanists who have seen it. Some of its peculiar characters are shared with the related and almost equally rare species, *T. spathulata*. This similarity led Larsen (1927) to consider *T. condensata* to be the same as *T. spathulata*. She stated (p. 23) that the head size is of no value for specific demarcation between the two species. This notion was occasioned by her confusion of material of a third species, *T. Parryi*, with these two. She reduced *T. condensata* and *T. Parryi* var. *alpina* (= *T. Parryi*) to *T. spathulata* apparently because the head size of the plants of *T. Parryi* was intermediate between the other two species. *Townsendia condensata* and *T. spathulata* may be distinguished by head size and by several other characters as well. These are given in tabular form below.

<i>Townsendia condensata</i>	<i>Townsendia spathulata</i>
Short-lived perennial.	Long-lived perennial.
With or without conspicuous caudex and often with conspicuous lateral stems.	With caudex densely matted with the old and new leaves.
Phyllaries acuminate.	Phyllaries acute or only slightly acuminate.
Primary heads large, involucres (of the primary heads, at least) more than 1.7 cm. wide.	All heads small, the involucres less than 1.6 cm. wide.

Townsendia condensata is known almost entirely from alpine, apomictic material. Fortunately, attention was called to a sexual population of the species in Park County, Wyoming when Heiser (1948) described *T. anomala*. The material on which Heiser's species is based is a little different from the alpine apomicts of *T. condensata*. However, the differences are only in the degree of pubescence and length of stems, and both of these characters vary from population to population in the apomicts. If *T. spathulata* had not been confused with *T. condensata* at the time of Heiser's investigation, he probably would have been able to associate his material with the latter species.

Sexual material of *T. condensata* probably will be found also in Fremont County, Wyoming. *Parry* 143, from the Wind River



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16

MAPS 15-16. 15. Geographic distribution of sexual and apomictic *Townsendia condensata* and sexual and apomictic *T. spathulata*. 16. Geographic distribution of *T. mexicana*.

Valley, is a single dried-up plant, but it is much like the presently-known sexual population in Park County. The Wind River Valley has a number of habitats similar to that in Park County where the sexual population is now known to occur. Further collections in western Wyoming will be required to solve the problems of location and diversity of sexual plants of this peculiar little species.

A feature not apparent in sexual material of *T. condensata* grown in its native habitat becomes apparent in greenhouse cultures. Under these conditions it does not remain a pulvinate little mass, but instead develops a single, erect, leafy stem which later branches at the base. This habit reveals a close, but otherwise not too obvious, relationship with *T. Parryi*. Once the similarity in habit has been noted, other indications of this relationship become more evident. Additional features the two have in common include the long-acuminate phyllaries, large heads, and bifurcate acheneal hairs.

16. *Townsendia spathulata* Nutt.

Townsendia spathulata Nutt. Trans. Am. Phil. Soc. 7: 305. 1840.
Type: Nuttall s.n., "On the Black Hills, (an alpine chain toward the sources of the Platte.)", 1834. (BM, holotype, examined by Dr. R. C. Rollins; CH!, PH!, isotypes).

Densely rosulate-pulvinate, taprooted perennial; caudex becoming several-branched, obscured by the dense tufts of new leaves and the persistent dead leaves; leaves spatulate, entire, acute or obtuse, mucronulate (usually hidden by the pubescence), densely pubescent with a villous-woolly or sericeous pubescence of simple, multicellular trichomes with conspicuous end-walls, 7-20 mm. long, 1.5-4 mm. wide; heads embedded in the leaves and appearing sessile but usually on very short peduncles not over 10 mm. long; involucres 8-16 mm. wide, 6.3-10 mm. high; phyllaries in 3-4 series, mostly lanceolate, sometimes narrowly ovate or elliptical, acute or very slightly acuminate, scarious- and lacerate-ciliate-margined, the cilia sometimes long and tangled, lightly or densely pubescent with long, simple, multicellular trichomes, 3-9 mm. long, 0.8-2.5 mm. wide; ray-florets ca. 12-30; ray-corollas pinkish, brownish orange, or lavender, often glandular on the abaxial surface, 2-3-toothed, 6-12 mm. long, 1.5-3 mm. wide; disk-corollas yellow and usually pinkish or reddish tinged, 3.8-5.3 mm. long; achenes oblanceolate, compressed, 2-ribbed, moderately pubescent with short, duplex, bifurcate or glochidiate hairs, densely papillose, 2.8-4.1 mm. long, 1-1.5 mm. wide; pappus of the ray- and disk-florets similar, of ca. 14-30 plurisetose, barbellate (sometimes with recurved barbs) bristles, deciduous in a ring around the apex of the achene, 4.5-6.2 mm. long. Reproduction sexual and apomictic. Fremont, Natrona, and Sweetwater Counties, Wyoming. Map 15. Plate XXIII, fig. 4.

Representative specimens. Wyoming. Fremont Co.: Beaver Hill, 32.5 mi. southeast of Lander, Beaman 880 (CH); 1 mi. south of Pa-

cific Creek, *Beaman* 883 (GH); open ridges, 1 mi. south of Pacific Springs, *Porter* 4544 (\dagger CH, \dagger RM, RSA, WTU); South Pass, Wind River Mts., 7650 ft. alt., *Ripley & Barneby* 7965 (* and \dagger CAS). Fremont Co. (?): Wind River, *Parry* 142 (F, GH, MO, NY, *PH, YU). Natrona Co.: 4 mi. west of Alcova, *Beaman* 878 (GH); on the Satanka Formation ca. 4 mi. west of Alcova, 5400 ft. alt., *Porter* 4428 (*DAO, GH, *RM, RSA, WTU). Sweetwater Co.: Bush Ranch (near Steamboat Mtn.), *Nelson* 7094 (\dagger RM).

Although *T. spathulata* and *T. condensata* are amply distinct species, they are closely related. The confused history of the two gives one indication of that relationship. The following similarities between the two give further indication: spatulate leaves, densely pubescent with long, simple, multicellular trichomes with conspicuous end-walls; bifurcate or entire achienial hairs (although some populations of *T. spathulata* have glochidiate hairs); very deciduous pappus; conspicuously papillose achenes. Even though sexual *T. condensata* seems to be rarer than *T. spathulata*, the former species is the more generalized type. *Townsendia spathulata* appears to have become specialized to conditions on the relatively arid plains of central Wyoming.

The type-localities of this and the other Nuttall species have been considered with the history of the genus. An additional feature, which concerns only this species, was merely mentioned there. In the specimen *Ripley & Barneby* 7956, from South Pass, Fremont County, Wyoming, two plants on the sheet differ in certain minor features from a third. A pollen examination revealed that the one represents apomictic and the other two sexual material. In examining the Nuttall type-material of this species in the British Museum, Dr. Rollins noted (on a slip of paper now with the Gray Herbarium material of *T. spathulata*): "I would say that there is the possibility of 3 of the 4 plants belonging to one thing and the other to another. The three are less dense, less woolly etc." In these same features the plants of *Ripley & Barneby* 7956 differ. The sexual plants are less dense and less woolly. In addition, the ray-corollas of the sexual plants are densely glandular and those of the apomicts are nearly glabrous. Also, the ray-corollas of the sexual plants are more fully expanded than are those of the apomicts. Is it possible that Ripley and Barneby have sampled the same populations of sexual and apomictic plants which yielded Nuttall's type-collection of this species?

It seems likely that Nuttall collected this species in more than one locality. The plants of the type collection in the British Museum are in flower. Nuttall's specimens in the Gray and Phila-

delphia Academy Herbaria are well past flowering. *Ripley & Barneby* 7956 in flower was collected on June 14 and *Porter* 4428 in flower was collected on May 9. Dr. Porter's material from near Alcova, Natrona County, Wyoming, grew at an elevation about 2000 ft. lower than South Pass where Ripley and Barneby made their collection. Possibly Nuttall first collected *T. spathulata* at a low elevation after it had flowered. As he proceeded west he may have obtained flowering material from some higher station. This higher station could be South Pass, through which his expedition traveled.

17. *Townsендia incana* Nutt.

Townsендia incana Nutt., Trans. Am. Phil. Soc. 7: 305. 1840.
Type: Nuttall s.n., "On the Black Hills, (an alpine chain toward the sources of the Platte.)", 1834 (BM, holotype, examined by Dr. R. C. Rollins; CH!, PH!, isotypes).

Townsендia Fremontii T. & G., Bost. Journ. Nat. Hist. 5: 106. 1845. Original material: apparently collected in Wyoming by Fremont on his first expedition in 1842 (CH).

Townsендia arizonica A. Gray, Proc. Am. Acad. 16: 85. 1880.
Type: Palmer 204 in 1877, Trumbull, Mohave Co., Arizona (*CH, lectotype; *MO, NY, US, syntypes).

Townsenda arizonica X incana M. E. Jones, Zoe 2: 248. 1891.
Type: Jones s.n., south Little Colorado, Navajo or Apache Co., Ariz., 9 June 1890 (*ROM, holotype).

Townsендia incana Nutt. var. *ambigua* M. E. Jones, Zoe 4: 264. 1893. A variety based on several vaguely designated collections.

Townsендia diversa Osterhout, Bull. Torr. Bot. Club 55: 75. 1928.
Type: Osterhout 6116, hills south of Grand Junction, Mesa Co., Colo. (*RM, holotype).

Pulvinate or suberect, taprooted, perennial (rarely biennial); caudex becoming much-branched, sometimes subterranean; stems mostly conspicuously canescent, sometimes long and much-branched; leaves narrow spatulate or oblanceolate, entire, acute, mucronate, moderately to densely stribose, up to 45 mm. long and 5 mm. wide; heads mostly terminal on the stems, infrequently pedunculate; involucres campanulate, 8-19 mm. wide, 7-14 mm. high; phyllaries in 3-4 (rarely 5) series, lanceolate, acute, scarious- and lacerate-ciliate-margined, strigose on the outer surface, 3-12 mm. long, 1-3.6 mm. wide; ray-florets ca. 10-30; ray-corollas mostly white on the adaxial surface and often with an abaxial median pink stripe, 7-13 mm. long, 1.5-3 mm. wide; disk-corollas yellow and often pink-tinged, 3.7-6.5 mm. long; achenes oblanceolate, compressed, 2-ribbed, pubescent with duplex, glochidiate hairs, 3.0-4.7 mm. long, 1.0-1.8 mm. wide; ray-pappus of ca. 15-30 plurisetose, barbellate bristles, 0.3-6.3 mm. long, often of different lengths on the same achene, not as long as the disk-pappus; disk-pappus of ca. 15-35 plurisetose, barbellate bristles, slightly exceeding the length of the disk-corollas. $2n = 18$ in sexual plants and $2n = 27, 28, 29$, ca. 30,

and 36 in apomictic plants. Central Wyoming southwest to Nevada and central Arizona. Map 14. Plate XXII, fig. 1.

Representative specimens. **Arizona.** Apache Co.: Water Lily Canyon, 35 mi. northeast of Kayenta, *Burton s.n.*, Aug. 1934 (\dagger NA); 5 mi. west of Rock Point, *Cutler 2196* (CAS, GH, \dagger MO, us); Navajo Indian Reservation, about the north end of the Carrizo Mts., *Standley 7332* (\dagger NY, us). Coconino Co.: ca. 24 mi. north of Flagstaff, *Beaman 971* (*GH); 6 mi. west of Grand Canyon Bridge, Marble Canyon, 3800 ft. alt., *Benson 129* (\dagger UC); Moqui Wash, 8 mi. west of Winslow, 5000 ft. alt., *Darrow 2699* (*CAS); 6 mi. south of Kaibito, Navajo Indian Reservation, 6300 ft. alt., *Darrow 2730* (\dagger CAS); U. S. Highway 89 along Vermilion Cliffs about 19 mi. east of Jacob Lake, *Ferris 10262* (\dagger DS); between Winslow and Flagstaff, *McKelvey 4507* (*GH); 15 mi. northeast of Tuba City, 5450 ft. alt., *Kearney & Peebles 12889* (\dagger MICH, POM); 2 mi. east of Ashfork, *Preece & Turner 2617* (*ws). Mohave Co.: brink of Toroweap Fault, Kanab Plateau, Grand Canyon National Monument, Toroweap, 6300 ft. alt., *Cottam 14026* (*UT); Hackberry, *Jones 4516* (DS, *NY, POM, RM, UC, US, UTC); Peach Springs, *Lemmon & Lemmon s.n.*, June 1884 (* and \dagger UC, *us). Navajo Co.: Betatakin, *Howell 24451* (*CAS); south of Winslow, *Peebles 9535* (*MICH); Monument Valley on the Utah-Arizona line, *Howell 24731* (\dagger CAS). Yavapai Co.: Clemenceau, W. W. *Jones s.n.*, 10 July 1922 (*UC); Smelter Grounds, W. W. *Jones s.n.*, 19 July 1922 (*MO, UC, US). **Colorado.** Delta Co.: Hotchkiss, 6000 ft. alt., *Cowen 337* (\dagger YU). Eagle Co.: McCoy's, *Osterhout 2761* (*RM); Eagle, *Osterhout 4716* (\dagger RM). Garfield Co.: mountain between Loma and junction to Varnal Highway, 6000-9000 ft. alt., *Cottam 5997* (\dagger UT); 3 mi. northwest of Carbondale, *Langenheim 2020* (\dagger COLO); west-facing slope, along Government Creek, 5 mi. north of Rifle, 1900 m. alt., *Weber 3319* (CAS, COLO, CS, \dagger RSA, UTC, ws). Gunnison Co.: hillside 15.6 mi. west of Gunnison on Highway 50, *Preece & Turner 2795* (\dagger ws). Grand Co.: Kremmling, *Osterhout 3497* (*RM). Mesa Co.: 1.4 mi. inside Colorado National Monument on road from Grand Junction, *Beaman 801* (\dagger GH); 1 mi. outside Colorado National Monument toward Glade Park, *Beaman 802* (*GH); Grand Junction, *Eastwood s.n.*, May 1891 (\dagger POM, us); 5 mi. west of Gateway in southern part of county, 4300 ft. alt., *Harrington 4362* (*COLO); Grand Junction, *Jones s.n.*, 15 April 1891 (\dagger POM); 4 mi. south of Mesa, 7800 ft. alt., *Rollins 2190* (DS, GH, *NA, *US, UTC). Moffat Co.: Craig, *Osterhout 5117* (\dagger RM); canyon near confluence of Green and Yampa Rivers, ca. 7000 ft. alt., *Porter 3620* (\dagger DS, GH, RM, UC, US, WTRU). Montezuma Co.: McElmo Creek, *Eastwood s.n.*, June 1892 (\dagger POM); entrance of Mesa Verde National Park, *Nelson 10419a* (GH, MO, \dagger NY, RM, UC). Montrose Co.: Naturita, 5400 ft. alt., *Payson 242* (CM, COLO, GH, MO, MONT, \dagger RM, ws); hills near Montrose, 5800 ft. alt., *Payson 657* (\dagger RM); Paradox, 5400 ft. alt., *Walker 90* (DS, GH, MO, NY, POM, \dagger RM, US); bench above San Miguel River, 24 mi. northwest of Naturita, *Weber 3566* (COLO, CS, DS, MONTU, OKL, PH, \dagger RM, RSA, UC,

UTC, ws). Rio Blanco Co.: south side of White River, 2 mi. southeast of mouth of Wolf Creek, 6000 ft. alt., *Graham* 9039 (CM, †NA); bluff by White River, 23 mi. east of Rangely, 5500 ft. alt., *Ripley & Barneby* 7783 (†CAS). San Miguel Co.: Norwood Hill, 7000 ft. alt., *Walker* 448 (DS, GH, †MO, NY, POM, RM, US); ridgetops, Gypsum Valley, 4 mi. east of Gypsum Gap, T 44 N, R 16 W, east of Gladel, *Weber* 4725 (†COLO, RSA, UC, WS, WTU). Nevada. Lincoln Co.: Panaca, *Jones* s.n., 6 Sept. 1912 (†POM); Cathedral Gorge, north of Panaca, 5000 ft. alt., *Ripley & Barneby* 6344 (†CAS). Nye Co.: Tonopah, 6000 ft. alt., *Shockley* 103 (†UC). New Mexico. McKinley Co.: Gallup, *Eastwood* 5628 (†CAS). Sandoval Co.: Jemez Biological Camp, Jemez Mts., *Castetter* 1170 (†RM). San Juan Co.: Aztec, *Baker* 729 (†MO, NY, POM, RM; US p.p., with 1 plant of *T. exscapa*). Utah. Beaver Co.: Frisco, *Jones* s.n., 1880 (*GH); Milford, 5000 ft. alt., *Jones* 1794 (CM, MO, *NY, PH, POM, US, UTC, *WS, YU). Carbon Co.: Price, *Flowers* F18-30 (*UT); Sunnyside, *Jones* s.n., 15 Nov. 1907 (†POM); 4 mi. north of Price, *Maguire & Maguire* 18342 (CAN, †NY, UTC). Daggett Co.: base of cliff, Sheep Creek, 12 mi. south of Manila, 6000 ft. alt., *Hitchcock et al.* 3913 (DS, NA, †WTU). Duchesne Co.: Myton, 5000 ft. alt., *Jones* s.n., 20 May 1908 (†POM). Emery Co.: ½ mi. north of the San Rafael River crossing along the Hanksville-Greenriver Road, *Holmgren, Boyle, & Will* 7768 (†UTC); Orangeville, 6000 ft. alt., *Jones* 5464c (POM, †US); first fork of Calf Springs Canyon, San Rafael Swell, *Maguire & Maguire* 18303 (GH, †NY, US, UTC, WS). Garfield Co.: wash east of Escalante, 5500 ft. alt., *Cottam* 4402 (†UC, UT); west slopes of Henry Mts., 5500 ft. alt., *Cottam* 5524 (†UT); open forest, northwest rim of Bryce Canyon, 8000 ft. alt., *Degener & Peiler* 16533 (†MO); 7 mi. east of Escalante, *Holmgren & Nielson* 7736 (†UC, UTC); 25 mi. southeast of Hanksville, Colorado River Rim, *Parry* s.n., 6 June 1941 (NY, †UTC); 5 mi. north of Hatch, 7000 ft. alt., *Ripley & Barneby* 8537 (†CAS). Grand Co.: Thompson, *Jones* s.n., 7 May 1891 (*POM); Westwater, 4400 ft. alt., *Jones* s.n., 28 June 1898 (†POM); Moab and vicinity, 1200-1500 m. alt., *Rydberg & Garrett* 8444 (†NY, RM, UC). Iron Co.: Cedar City, *Parry* 94 (CH, †MO, YU). Kane Co.: 8 mi. north of Kanab, *Eastwood & Howell* 9270 (†CAS); 2 mi. east of Zion Park, east entrance, Highway 15, *Preece & Turner* 2510 (†WS). Piute Co.: Marysvale, 7000 ft. alt., *Jones* 5355q (†US). San Juan Co.: at Natural Bridge north of Montecello, *Clover & Jotter* 2007 (†MICH); without definite locality, 4300 ft. alt., *Cottam* 5816 (*NA); along San Juan River, near Bluff, 1200-1500 m. alt., *Rydberg & Garrett* 9962 (NY, RM, †UT). Sevier Co.: near Belknap, 6000 ft. alt., *Stokes* s.n., 10 June 1900 (†DS, NY, US); Richfield, 5500 ft. alt., *Ward* 176 (GH, †MO, PH, US). Uintah Co.: hills east of Dinosaur National Monument, 5000 ft. alt., *Graham* 7563 (CM, †NA); ridge, east side of Green River, Island Park, 5000 ft. alt., *Graham* 9194 (CM, †MO, NA). Wayne Co.: plains, edge of Green River Desert about 5 mi. northeast of Hanksville, ca. 1500 m. alt., *McVaugh* 14563 (CAS, †NY); Fruita Arch Canyon, Ma-

guire & Maguire 18123 (CH, NY, US, †UTC). Wyoming. Fremont Co.: canyon side above Wind River, 16 mi. southeast of Dubois, Beaman & Preece 507 (†ws); hillside near Black Buttes Mill Site, 20 mi. north of Shoshoni, 5200 ft. alt., Freytag 78 (†RM); Badwater (probably Badwater Creek near Lysite), Nelson s.n., 26 June 1910 (†RM); Riverton, Nelson s.n., May 1920 (†RM). Natrona Co.: 4 mi. west of Alcova, Beaman 875 (†CH); Alcova, Gooodding 166 (†MO, RM, US). Sweetwater Co.: 6 mi. north of McKinnon, Goodman 3105 (†MO, †NY); hills near Rock Springs, 6200 ft. alt., Larsen 17 (†RM); Granger, Nelson 4622 (CH, †MO, NY, RM, US). Uinta Co.: Ft. Bridger, Nelson 4599 (CM, CS, MONT, †NY, POM, RM).

Apomicts of *T. incana* usually are easy to determine as that species; sexual populations sometimes are more difficult. A mostly-sexual geographic segment of this species which has long caused taxonomic difficulties is located in northern Arizona. Gray described these plants as *T. arizonica* and distinguished them from *T. incana* by their long ray-pappus. Subsequently, long-ray-pappus forms of *T. incana* from many parts of its range were referred to *T. arizonica*. It is evident from the material now available that the ray-pappus length is much too variable to be a useful taxonomic character in *T. incana*.

Larsen (1927) accepted *T. arizonica* and referred some of the western Colorado specimens of *T. incana* to *T. arizonica*. Her key was designed to separate the two by leaf length and shape. However, the vigor of the plant influences these characters which are not constant, even in obligate apomicts. In addition, Larsen did not distinguish *T. annua* and *T. Fendleri* from *T. strigosa*, and her key does not satisfactorily separate many specimens of *T. strigosa* (as she understood it) from *T. incana*.

The most atypical portion of *T. incana* is represented by three sexual collections, Rollins 2190 and Osterhout 2761 and 3474, from northwestern Colorado. The habit of these plants is unlike that of typical *T. incana*. The former have short, thick caudices, not unlike *T. exscapa*. The heads, borne on short peduncles, are somewhat embedded in the tufts of leaves. In their other features these plants are characteristic of *T. incana*. They are from relatively high elevations and possibly represent elevational and geographic polymorphy in *T. incana*.

Another sexual population which diverges from typical *T. incana* is Jones 1794 from Beaver County, Utah. These plants are distinctive because of their reduced size and very heavy, crenescens pubescence. The apomicts in this area are morphologically more typical of *T. incana*.

A small amount of variation in *T. incana* is not attributable to geographic differentiation. In San Juan County, Utah two collections, Cottam 5816 and Holmgren 3183, are intermediate between *T. annua* and *T. incana*. Although these plants seem to be short-lived perennials, their general aspect is that of *T. annua*. The disk-pappus of Holmgren 3183 is shorter than the disk-corollas, a characteristic of *T. annua*. The stems are canescent, and the phyllaries are in 4-5 series, characteristic of *T. incana*. Hybridization of the two species in this area therefore seems probable.

The ranges of *T. incana* and *T. annua* overlap in an extensive area, and their flowering periods coincide. Probably they are at least partly interfertile. Herbarium material, however, suggests that hybridization is very rare. The great abundance of apomixis, or more directly, the rarity of sexual material of *T. incana* probably restricts the frequency of hybridization between these two species.

It is possible that some of the *T. incana* populations in Mesa County, Colorado and Grand County, Utah have been affected through hybridization with *T. strigosa*. Several collections from this area are of suberect plants, characteristic of *T. strigosa* but not of *T. incana*. However, since some of the best characters for distinguishing these two species involve the habit, it is very difficult, with as variable a species as *T. incana*, to be reasonably sure, on the basis of herbarium specimens, that hybridization has occurred. Jones s.n., 7 May 1891 (Grand Co., Utah) is an example of possible crossing. Five plants of this collection (POM 39664) are fairly typical *T. incana*. A sixth plant has a swollen root-stem junction with persistent, broad basal leaves, resembling *T. strigosa*. This plant retains the canescent pubescence of *T. incana*.

Townsendia incana occurs at elevations from approximately 4000 to 8000 ft. It is especially abundant on the Colorado Plateau in sandy soils amidst junipers and piñons. It flowers in the spring and summer at times when sufficient moisture is available, usually in May and early June. Some flowering material, however, has been collected in April, July, August, and September. All material which has been available for greenhouse and garden cultures exhibits a more or less indeterminate flowering period. Some plants lived and flowered in the greenhouse for as long as two years.

Townsendia incana is most closely related to *T. Fendleri*. The latter was probably derived from ancestral stock nearly or quite like the former species. No other species are very closely related to these two.

18. *Townsendia Fendleri* A. Gray

Townsendia Fendleri A. Gray, Mem. Am. Acad. 4 (Pl. Fendl.): 70. 1849. Type: *Fendler* 350, gravelly hillsides, Santa Fé, Santa Fé Co., New Mexico, May-July 1847 (GH, holotype; MO, UC, isotypes).

Cauliflous, decumbent or suberect, or infrequently rosulate, taprooted perennial (or sometimes biennial?); caudex becoming much-branched, often subterranean; stems much-branched, short or becoming elongate, stri-gose or pilose-strigose, sometimes canescent, up to 3 dm. long; leaves narrowly oblanceolate to nearly linear, entire, acute, mucronate, mostly involute, strigose, up to 35 mm. long and 3.5 mm. wide; heads terminal on the stems; involucres campanulate, 6.4-13 mm. wide, 5.0-8.5 mm. high; phyllaries in 4-5 series, lanceolate or ovate-lanceolate, acute, ciliate and broadly scarious-margined, strigose on the outer surface, 2.7-8 mm. long, 1-3 mm. wide; ray-florets ca. 10-25; ray-corollas white on the adaxial surface and with an abaxial pinkish or blue-purplish streak, 4.8-10 mm. long, 1-2.5 mm. wide; disk-corollas yellow, infrequently pinkish-tinged, 2.0-3.5 mm. long; achenes oblanceolate, compressed, 2-ribbed, 2.1-3.2 mm. long, 0.8-1.2 mm. wide, pubescent with duplex, glochidiate hairs; ray-achenes more densely pubescent than those of the disk, papillose (the disk-achenes infrequently minutely papillose); ray-pappus of connate-coroniform squamellae or short, plurisetose bristles up to 1.5 mm. long; disk-pappus of ca. 15-25 plurisetose, barbellate bristles, 2.4-3.5 mm. long, shorter than the disk-corollas. Reproduction sexual. South-central Colorado and north-central New Mexico. Map 4. Plate XXII, fig. 2.

Representative specimens. **Colorado.** County unknown: valley of the Arkansas, *Wolf* 517 (F, POM, US). Chaffee Co.: Salida, *Baker, Earle & Tracy* 1016 (F, MO, NY, POM, US); Salida, *Osterhout* 3424 (DS, GH, NY, POM, *RM); Arkansas River near Poncha Pass, *Jones* 767 (CAS, CM, COLO, DS, GH, *MO, NY, OC, POM, UTC); hills southeast of Buena Vista, lower end of Trout Creek Cr., *Penland* 4352 (COLO); ridge along the Arkansas River, 8 mi. northwest of Salida, *Waterfall* 11511 (OKL, RSA, *UC). Fremont Co.: Texas Creek, *Brandegee* 951 (MO, PH, UC); sandbar, Canon City, 5280 ft. alt., *Brandegee* s.n., June 1876 (*UC). Huerfano Creek, *Brandegee* 1294 (GH, MO, UC). Pueblo Co.: Pueblo, *Bethel* s.n., 2 July 1897 (*CS). **New Mexico.** Rio Arriba Co.: Ghost Ranch, Rio Chama drainage, *Goodwin* s.n., 24 Aug. 1932 (*GH); 13 mi. south of Cebolla, *Ripley & Barneby* 10294 (CAS); Ojo Caliente, 6000 ft. alt., *Smith* s.n., 27 Aug. 1894 (PH). Sandoval Co.: 6 mi. west of San Ysidro, 5500 ft. alt., *Ripley & Barneby* 8344 (*CAS); San Ysidro, *Nelson* 11619 (*RM, UC). Santa Fé Co.: Santa Fé, *Degener* 4689 (NY); near Espanola, 5600 ft. alt., *Heller & Heller* 3547 (ND, NY; US p.p., with 1 plant of *T. annua*); 2 mi. north of Santa Fé, ca. 7000 ft. alt., *Hitchcock et al.* 4186 (NA, *WTU).

Since Larsen (1927) made no distinction between *T. annua* and *T. strigosa*, and considered *T. Fendleri* a worthless taxon, she reduced the latter to *T. strigosa*. Her confusion, of course, was between *T. annua* and *T. Fendleri*. No modern material of these

species is difficult to determine. However, some of the specimens she had, especially *Brandegee* 951 and *Jones* 767 have considerably longer stems than is usual for *T. Fendleri*. In addition, on one sheet she examined (MO 121087) *Brandegee* 951 was accompanied by the following undated scribbled note in Gray's handwriting: "951 fits much of my *Townsendia strigosa* well. I dare say *Fendleri* will not be very Im'pt!" This note, and the poor specimens mentioned above, must have influenced Larsen to reduce *T. Fendleri*. In the confusion, *Brandegee* 1094 further complicates matters; MO 121070 with the number 1094 is clearly *T. Fendleri*. *Brandegee* 1094 in the New York Botanical Garden Herbarium and the Philadelphia Academy Herbarium is clearly *T. annua*. A *Brandegee* collection in the Gray Herbarium without a number but with essentially the same label data "Adobe plains, San Juan R." is also *T. annua*. *Brandegee* 1294 (GH, MO 121088, UC) Huerfano Creek, Huerfano Co., Colo., is *T. Fendleri*. It is probable that *Brandegee* 1094 is not actually a mixed collection of the two species. Very likely, because of the similarity of the numbers 1094 and 1294, the label 1094, with its accompanying data, was erroneously transferred to specimen MO 121070 which should be *Brandegee* 1294. The high degree of similarity of the two plants on this sheet to *Brandegee* 1294 supports this idea. Moreover, it is improbable that *T. Fendleri* occurs on the "adobe plains" of the San Juan River valley.

In most areas, and in most collections, *T. Fendleri* and *T. annua* are easily distinguishable. But around Santa Fé, New Mexico, where their ranges overlap, the two species closely resemble each other. *Townsendia Fendleri* especially seems to approach *T. annua*. The mixed collection, *Heller & Heller* 3547 from near Santa Fé, indicates a considerable similarity of the two.² *Townsendia Fendleri* is probably not a perennial in that area, while it is in the other portions of its range. In northern New Mexico it may have obtained genes for a shorter life-cycle from *T. annua*. Except in that area the two species probably are fairly well isolated geographically. *Townsendia Fendleri* occurs at moderate elevations mostly within the piñon-juniper belt while *T. annua* occurs at lower elevations below the piñons and junipers.

Although *T. annua* and *T. Fendleri* have been confused because of their similarity, the closest relationship of *T. Fendleri* seems to be with *T. incana*. These two species are allopatric (considering the range of the sexual forms of *T. incana* only)

² *Heller & Heller* 3547 in MO, MSC, and US p.p. is of *T. annua*; in ND, NY, and US p.p., this collection is made up of plants of *T. Fendleri*.

and *T. Fendleri* probably is a specialized, reduced form from more generalized *T. incana* stock. The habit of the two species (at least of some forms of *T. incana*) is almost identical. The differences are mainly quantitative ones, paralleling those between *T. strigosa* and *T. annua*.

19. *Townsendia strigosa* Nutt.

Townsendia strigosa Nutt. Trans. Am. Phil. Soc. 7: 306. 1840.
Type: Nuttall s.n., "On the Black Hills, (or eastern chain of the Rocky Mountains,) near the banks of the Platte.", 1834 (BM, holotype, examined by Dr. R. C. Rollins; CH!, PH!, isotypes).

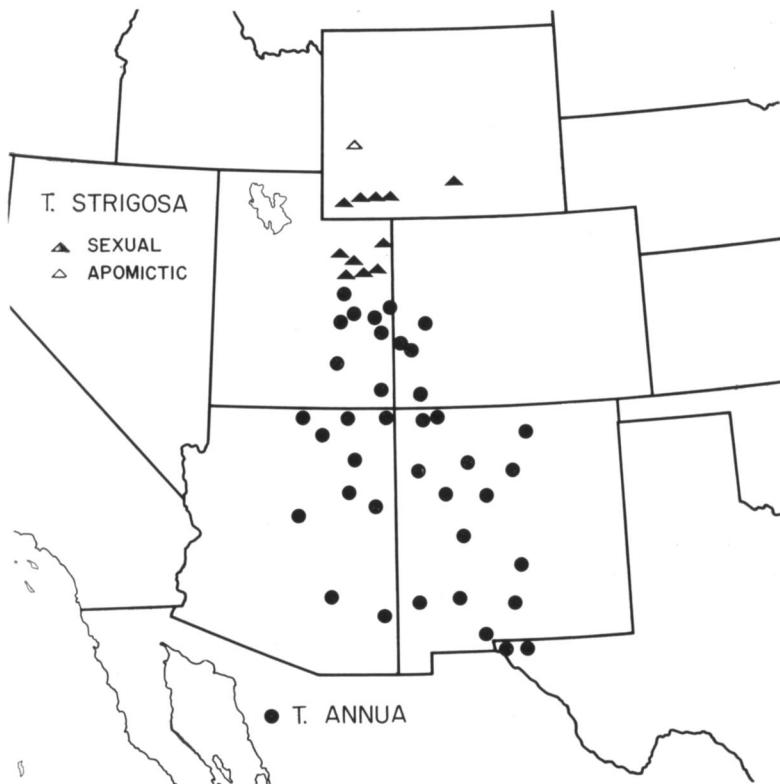
Townsendia incana Nutt. var. *prolixa* M. E. Jones, Contrib. West. Bot. 13: 15. 1910. Type: Jones s.n., Chepeta Well, Uintah Co. (?), Utah, 6000 ft. alt., 23 May 1908 (*POM, holotype).

Caulescent, taprooted biennial; root-stem junction enlarged; stems branched at the base, few to moderately numerous, branched again just below the heads in a cymose manner, mostly spreading-suberect, usually red with cyanic pigments, striate, strigose-pilose, up to 2 dm. long; basal leaves persistent, oblanceolate or spatulate, entire, mucronate, obscurely 1-3-nerved, lightly to moderately strigose on both surfaces, up to 45 mm. long and 7.0 mm. wide; caulinne leaves similar, smaller, often clustered immediately below and overtopping the fastigiate heads; involucres 5-20 mm. wide, 5-10 mm. high; phyllaries in 3-4 series, elliptic-ovate to lanceolate, acute or rarely slightly acuminate, with broad, scarious, lacerate-ciliate margins, 2.5-9 mm. long, 1.5-3.0 mm. wide, the inner longer than the outer, the outer moderately strigose on the abaxial surface, the inner only slightly if at all pubescent near the mid-axes and apices; ray-florets ca. 12-30; ray-corollas white to pink, often darker near the base and with a darker longitudinal streak on the abaxial surface, 5-14 mm. long, 1.5-2.8 mm. wide; disk-corollas yellow or mottled with pink, 3.3-5.0 mm. long; achenes oblanceolate, compressed, 2-ribbed, those of the ray-florets rarely 3-ribbed, moderately pubescent with duplex, glochidiate hairs, those of the ray-florets generally slightly more pubescent than those of the disk-florets, both generally papillose, 3.0-4.0 mm. long, 0.8-1.3 mm. wide; pappus of the ray-achenes of short, plurisetose, barbellate bristles mostly connate at the base, rarely exceeding 1.6 mm. in length; pappus of the disk-achenes of ca. 20-35 plurisetose, barbellate bristles, 3.3-5.5 mm. long, mostly equalling or slightly exceeding the length of the disk-corollas, rarely shorter. Reproduction mostly sexual, rarely apomictic. Northeastern Utah and southwestern Wyoming, probably also in adjacent northwestern Colorado. Map 17. Plate XXII, fig. 3.

Representative specimens. Utah. Carbon Co.: 9-mile Canyon, 5000 ft. alt., Jones s.n., 22 May 1896 (*POM). Duchesne Co.: north of Duchesne along the Victory Highway, Osterhout 6196 (*RM). Uintah Co.: 5 mi. northwest of Dinosaur National Monument, 5500 ft. alt., Graham 7671 (*NA p.p., with 2 fragments of *T. incana*); bench west of Green River, south of mouth of Sand Wash, 5000 ft. alt., Graham 7946 (CM, *NA); eastern slope of Big Pack Mountain, west of Willow

Creek, Thorne's Ranch, Uinta Basin, 5500 ft. alt., *Rollins* 1705 (*^{GH}, NY). **Wyoming.** Carbon Co.: Solon, *Williams* s.n., July 1897 (*^{RM}). Sublette Co.: roadside, Big Piney, *Payson & Payson* 4350 (†^{GH}, MO, MSC, PH, †^{RM}, ws). Sweetwater Co.: Green River, *Nelson* 3031 (*^{GH}, ILL, MO, NY, *^{RM}, us); Green River, *Nelson* 4724 (*^{CM}, CS, MONT, POM, WS); 21 mi. west of Green River, *Payson & Armstrong* 3205 (GH, ILL, MO, MSC, PH, POM, *^{RM}); desert about 40 mi. south of Rock Springs, on the Hiawatha road, *Porter* 4573 (DAO, GH, *^{RM}, RSA, WTU). Uinta Co.: 6 mi. out of Mountainview toward Lonetree, *Holmgren & Tillett* 9474 (*UC, UTC); hillside near Lyman, 6500 ft. alt., *Rollins* 1636 (DS, *NA, US, ws).

Townsendia strigosa is not restricted to the Green River shales, but it occurs mostly within the bounds of the Green River formation in northeastern Utah and southwestern Wyoming. From the



MAP 17. Geographic distribution of *Townsendia annua* and sexual and apomictic *T. strigosa*.

observations of Mr. and Mrs. W. L. Bartholomew (personal communication), residents of the Uinta Basin of Utah, I have learned that the species is abundant in that area. It flowers in May and early June, and often occurs in fairly dense, conspicuous stands. It sometimes is mixed among apomictic plants of *T. incana* and sometimes occurs in pure stands. Sheep browse the plants, and by the end of June scarcely any standing plants are to be found.

Some variation in this species, especially near Green River, Wyoming, suggests hybridization with *T. annua*. Most of the plants of Nelson 3031 and 4724 have the disk-pappus shorter than the disk-corollas. Some plants have ovate phyllaries, in others the phyllaries are merely broadly lanceolate. The short disk-pappus and ovate phyllaries are characters of *T. annua*. One other specimen, Jones s.n., 22 May 1896, from Carbon County, Utah, very close to the range of *T. annua*, also has ovate phyllaries. Although *T. strigosa* and *T. annua* are allopatric, hybridization could be expected between them. Their ranges adjoin and there is no geographic barrier. They are very similar and probably have no strong genetic barriers to interbreeding.

Townsendia strigosa is closely related to *T. annua*, which is an evolutionarily more advanced species. The two have no other very close relatives. *Townsendia strigosa* superficially resembles *T. florifer* but is readily distinguished from that species by its glochidiate rather than bifurcate achenial hairs. It has been confused with *T. incana*; however, these two species are distinct enough so that no confusion is necessary.

As might be expected in a biennial, apomixis is unimportant in *T. strigosa*. It is interesting, but of minor significance, that the only known apomictic collection is from the northernmost station in the range of the species.

20. *Townsendia annua* Beaman, sp. nov.

Type: Maguire 13509, sand bed of Cottonwood Wash, vicinity of Wayland's Ranch, 1½ mi. north of Bluff, San Juan Co., Utah, April 19, 1936 (*GH, holotype; CAN, PH, UC, UTC, WTRU, isotypes).

Cauliflorous, taprooted annual; stems few to numerous, prostrate to ascending, branching at the base and above, minutely striate, strigose, 0.2-2.5 dm. long; basal leaves short-lived, oblanceolate or spatulate, entire, often mucronate, lightly strigose on both surfaces, up to 3 cm. long; cauline leaves similar to, but usually slightly smaller than, the largest basal leaves, longer-persistent, more or less evenly distributed on the stems, but appearing clustered on young branches below unexpanded heads, usually not surpassing expanded heads; heads terminating the leafy stems, or pedunculate on inconspicuous peduncles; involucres 8-16 mm. wide, 4.5-7.5 mm. high,

broadly expanded at maturity; phyllaries in 3, rarely 2-4, series, elliptical, obovate or ovate, obtuse, acute, or rarely slightly acuminate, the margins scarious and ciliate at least above, 2-6.7 mm. long, 1-2.6 mm. broad, the outer shorter than the inner, lightly or rarely moderately strigose-pilose on the outer surface, the inner series nearly or entirely glabrous; ray-florets ca. 12-30; ray-corollas white to pink or light lavender, often with a darker longitudinal streak on the abaxial surface, 5-9 mm. long, 1.5-2.7 mm. wide; disk-corollas yellow, sometimes pink- to purple-tipped, 2.3-3.7 mm. long; achenes oblanceolate to obovate, compressed, 2-ribbed, those of the ray-florets rarely 3-ribbed, lightly to moderately pubescent with duplex, glochidiate hairs, those of the ray-florets often slightly more pubescent than those of the disk-florets, both, especially those of the ray-florets, often papillose, 2.0-2.8 mm. long, 0.6-1.2 mm. wide; pappus of the ray-achenes of short, plurisetose, barbellate bristles, rarely exceeding 1 mm. in length; pappus of the disk-achenes of ca. 15-28 plurisetose, barbellate bristles, 1.8-3.0 mm. long, very rarely equaling the length of the disk-corollas. Reproduction sexual. East-central Utah south to southern Arizona, New Mexico, and Texas, probably in adjacent northern Mexico. Map 17. Plate XXII, fig. 4.

Herba annua. Caules decumbentes, pauci ad numerosi, striati, strigosí, 0.2-2.5 dm. longi; foliis inferioribus oblanceolatis vel spathulatis, integerimis, strigosis, fluxibus, superioribus similibus, minoribus et vivacioribus; pedunculis usque 5 cm. longis, strigosis. Involucrum 8-16 mm. latum, 4.7-7.5 mm. altum, maturitate aperiens; involuci squamis plerumque 3-seriatis, oblongis vel ovatis, 2-6.7 mm. longis, 1-2.6 mm. latis; achaenii oblanceolatis vel obovatis, compressis, aliquanto pubescensibus cum pilis glochidiatis, 2.0-2.8 mm. longis, 0.6-1.2 mm. latis; radii pappo semper breve, squamelato (squamellis coroniformibus); disci pappo plurisetoso, quam disci corollae plerumque breviore.

Representative specimens. **Arizona.** Apache Co.: Four Corners, 5000 ft. alt., *Deaver* 4037 (CAS); low hills just north of Petrified Forest, near the Rio Puerco, *Nelson & Nelson* 2144 (*RM). Coconino Co.: 10 mi. south of Navajo Bridge across the Colorado River, 4000 ft. alt., *Rollins & Chambers* 2432 (DS, GH, NA, UC, US, UTC); Cameron to Tuba City, 4700 ft. alt., *Peebles & Fulton* 11827 (CAS, *NY, US). Graham Co.: Tanque, 1200 m. alt., *Eggleson* 19872 (GH, US); Diversion Works in Freeman flat, 5 mi. southwest of Safford, *Maguire & Maguire* 10094 (*UTC). Navajo Co.: between Kayenta and Betatakin, *Eastwood & Howell* 6575 (CAS); between Winslow and Holbrook, *McKelvey* 4561 (GH); Holbrook, *Ward* s.n., 15 June 1901 (NY, US). Pinal Co.: near Dudleyville, *Griffiths* 3673 (NA). Yavapai Co.: Beaver Creek, *Purpus* 8300 (MO, UC, US). **Colorado.** Delta Co.: between Delta and Grand Junction, 4800 ft. alt., *Penland* 1763 (CAS, RSA). Montezuma Co.: Mancos, southwestern Colo., *Eastwood* s.n., June 1890 (COLO). Montrose Co.: Paradox, 5400 ft. alt., *Walker* 93 (GH, ILL, MO, NY, POM, *RM, US, WS, W TU); Naturita, 5400 ft. alt., *Payson* 321 (CM, COLO, DS, F, MO, MONT, *RM, WS). **New Mexico.** Bernalillo Co.: plains near Albuquerque, *Palmer* 31206 (MO, PH). Dona Ana Co.: Mesilla Valley, near Mesilla, *Standley* s.n., 23 May 1906 (*US); Mesilla Valley, 3850 ft. alt.,

Wooton & Standley s.n., 2 April 1907 (DS, F, MO, NY, *RM, US). Grant Co.: Mangas Springs, 18 mi. northwest of Silver City, 4300 ft. alt., *Metcalfe* 15 (CAS, DS, GH, ILL, MO, NY, POM, *RM, UC, US). Lincoln Co.: Carrizoza, *Earle* 607 (NY). McKinley Co.: along Highway 66, 15 mi. east of Gallup, *Nelson & Nelson* 2174 (MO, NY, *RM, UTC). Otero Co.: desert, just outside entrance to White Sands National Monument, *Goodman & Waterfall* 4987 (OKL). San Juan Co.: Aztec, *Baker* 728 (F, GH, MO, ND, NY, POM, *RM, US); 2 mi. northwest of Waterflow, *Cutler* 3331 (*MO, NA, US). Sandoval Co.: Torreones arroyo, *Keesecker* 38 (OKL). Santa Fé Co.: Santa Fé, *Fendler* 351 (GH, MO, PH); near Espanola; 5600 ft. alt., *Heller & Heller* 3547 (*MO, MSC; US p.p., with 2 plants of *T. Fendleri*). Sierra Co.: Hillsboro, north of Percha, 5500 ft. alt., *Metcalfe* 1510 (CAS, F, GH, MO, NY, POM, UC, US). Socorro Co.: Datil Forest, above Walter Medley's Ranch, ca. 9 mi. north of Magdalena, *Eggleson* 16197 (MO). Taos Co.: Taos, 6900 ft. alt., *Castetter* 1302 (*RM). Valencia Co.: Mount Taylor, between coal mine and Grants, 7000 ft. alt., *Parker* 2318 (RSA, UC). Texas. El Paso Co.: El Paso, 3700 ft. alt., *Ripley & Barneby* 4211 (CAS). Hudspeth Co.: in a basin between hills, 4 mi. east of Hueco, *Waterfall* 3867 (GH). Utah. Emery Co.: Green River, *Jones* s.n., 9 May 1890 (*MO, MSC, POM, UC, US); Mounds, *Jones* s.n., 5 Sept. 1901 (POM); Red Knoll enclosure, vic. Buckhorn Reservoir, San Rafael Swell, *Maguire* 18493 (GH, NY, US, UTC, WS; WTU p.p., with 1 plant of *T. incana*). Garfield Co.: Henry Mts., 5000 ft. alt., *Stanton* 1059 (UT). Grand Co.: 5 mi. south of Crescent Junction, *Holmgren & Hansen* 3295 (CAN, GH, IDS, *MO, NY, UC, US, UTC, WS, WTU); Westwater, *Jones*, s.n., 20 May 1901 (POM); Moab and vicinity, 1200-1500 m. alt., *Rydberg & Garrett* 8441 (NY). San Juan Co.: Cottonwood Wash, vicinity of Wayland's Ranch, 1½ mi. north of Bluff, *Maguire* 13509 (CAN, *GH, PH, UC, UTC, WTU).

Previously this species has been identified as *T. strigosa*.³ It is indeed closely related to that species. The present material, however, is separable into two clear-cut groups, each with its own range of variation which hardly overlaps that of the other. *Townsendia annua* and *T. strigosa* may be distinguished by the characters tabulated below.

In addition to the differences indicated in the table above, there are others which do not lend themselves to tabulation. *Townsendia annua* is more delicate in appearance and has very slender branches. On herbarium specimens it usually has no anthocyanin in the stems while *T. strigosa* usually does. The phyllaries of *T. annua* usually are shorter and broader with more conspicuously lacerate margins than are those of *T. strigosa*.

³ Nuttall's type material of *T. strigosa* in American herbaria is rather depauperate. Superficially, his plants do closely resemble *T. annua*. It is not surprising, therefore, that the two species previously have not been distinguished.

<i>Townsendia annua</i>	<i>Townsendia strigosa</i>
Annual.	Biennial.
Basal leaves soon deciduous.	Basal leaves persistent.
Root-stem junction not enlarged.	Root-stem junction enlarged.
Phyllaries mostly in 3, rarely 4, series.	Phyllaries mostly in 4, rarely 3, series.
Disk-corollas 2.3-3.7 mm. long.	Disk-corollas 3.3-5.0 mm. long.
Achenes 2.0-2.8 mm. long.	Achenes 3.0-4.0 mm. long.
Disk-pappus 1.8-3.0 mm. long, usually shorter than the disk-corollas.	Disk-pappus 3.3-5.5 mm. long, about equal to or longer than the disk-corollas.

Aside from the purely morphological evidence for this species being a true annual, the flowering time also gives that indication. Specimens in flower collected in every month from February to October are included in the present material. May and June collections are most frequent.

Townsendia annua appears to be derived from a prototype nearly or entirely similar to *T. strigosa*. The distinguishing characteristics of *T. annua* are mostly quantitative, reduced features of *T. strigosa*. The comparative measurements in the table above suggest this fact. *Townsendia annua* probably has become specialized for a somewhat more xeric existence than that of *T. strigosa*. This adaptation has come about primarily by development of the annual habit and correlation of the flowering season with the availability of water.

Putative hybridization of *T. annua* with *T. strigosa* is considered in the discussion of the latter species; that with *T. incana* under the discussion of *T. incana*, and that with *T. Fendleri* under the discussion of that species.

21. *Townsendia mexicana* A. Gray

Townsendia mexicana A. Gray, Mem. Am. Acad. 4 (Pl. Fendl.): 70. 1849. Type: Gregg s.n., Saltillo, Coahuila, Mexico, March 1847 (CH, holotype; MO, NY, isotypes).

Low, caulescent, taprooted perennial; stems often slightly woody at the base, loosely branched from the base upward, usually decumbent, sometimes terminally ascending and suberect, strigose-sericeous, up to 2.0 dm. long; leaves more or less evenly distributed on the stems, linear to narrowly oblanceolate, acute, mucronate, entire, or with 1-2 small lateral lobes near the tip, strigose, 5-25 mm. long, 0.4-2.5 mm. wide; peduncles solitary or rarely 2-3 at the ends of the branches, strigose, densely so near the head; involucres 6-12 mm. wide, 3.5-7.0 mm. high, broadly expanded at maturity; phyllaries in 2 (rarely 3) series, elliptic-obovate, scarious-margined, ciliate

near the obtuse-rounded (rarely acute) apices, the outer 2.5-4.5 mm. long, 0.5-2.2 mm. wide, lightly to moderately strigose on the abaxial surface, the inner 3.5-6.0 mm. long, 0.8-2.4 mm. wide, lightly strigose to nearly glabrous; ray-florets ca. 15-35; ray-corollas white on the adaxial surface and sometimes with a pink to purple median stripe on the abaxial surface, 5-10 mm. long, 1-1.7 mm. wide; disk-corollas yellow, the tips sometimes pink-purple, 1.8-3.4 mm. long; achenes ob lanceolate, compressed, 2-ribbed, moderately to lightly pubescent with duplex, glochidiate hairs, ray-achenes more pubescent than those of the disk, both or only the ray-achenes papillose, 1.8-2.7 mm. long, 0.5-1.2 mm. wide. $2n = 18$. Reproduction sexual. Southern Coahuila south to Mexico D. F., Mexico. Map 16. Plate XXIII, fig. 1.

Representative specimens. MEXICO. Coahuila. Ca. 3 mi. southwest of Saltillo, Beaman 1002 (*GH); Saltillo, Palmer 499 in 1880 (*MO, NY, US, YU); valley 15 kms. west (?) of Conception del Oro just within Coah. border, 2300 m. alt., Stanford, Rutherford & Northcraft 509 (DS, GH, *MO, NY, UC, WTU). Distrito Federal. Vicinity of Rancho de Flores near San Pablo, 15 mi. south of Mexico City, 7350-7600 ft. alt., Happ 296 (*MO). Hidalgo. El Arenal, slopes at Km. 100 Pan American (Laredo) highway south of Actopan, 2500 m. alt., Moore 1395 (*GH, UC); bluffs near Tula, 6800 ft. alt., Pringle 6573 (CAN, CAS, CM, F, GH, MEXU, MO, MSC, ND, *NY, PH, UC, US). Nuevo León. 17 mi. southeast of Galeana, Schneider 1115 (F). Querétaro. Near Higuerrillas, Rose et al. 9791 (GH, US). San Luis Potosí. Estacion Catorce, Sierra Madre Oriental, 2000-2100 m. alt., Pennell 17575 (PH, US). Tamaulipas. Near reservoir of Miquihuana at base of hills, Stanford, Taylor & Lauber 2384 (UC, WTU). Zacatecas. Between La Honda and Santa Rita via Pinos, Johnston 7472 (*GH, US); near Concepcion del Oro, Palmer 252 in 1904 (F, GH, MO, NY, US).

This Mexican endemic probably is the most highly evolved species of *Townsendia*. Its diminutive size, two series of phyllaries, very short ray- and disk-corollas, short pappus, and small achenes all are features of reduction. It is the only member of the genus with lobed leaves. All of its meiotic chromosomes are distinctly smaller than those known in any other species of *Townsendia* (cf. Plate I, fig. 3).⁴ *Townsendia mexicana* has no very close relatives but belongs with the group of species which include *T. incana*, *T. Fendleri*, *T. strigosa*, and *T. annua*. *Townsendia Fendleri*, *T. annua*, and *T. mexicana* exhibit a very strong parallel development.

The range of *T. mexicana* probably coincides with the occurrence of alkaline soils in central Mexico between the elevations of ca. 5000-8000 ft. It has been collected in flower from March to September.

⁴ Unfortunately, the chromosomes of *T. annua*, a species which shares many reduced features with *T. mexicana*, have not yet been examined.

SPECIES EXCLUDED FROM TOWNSENDIA

Townsendia Wrightii A. Gray, Bot. Mex. Bound. Surv. p. 78. 1859.
 = *Aster Wrightii* A. Gray, Smithson. Contrib. Knowl. 5 (Art. 6): 75. 1853.

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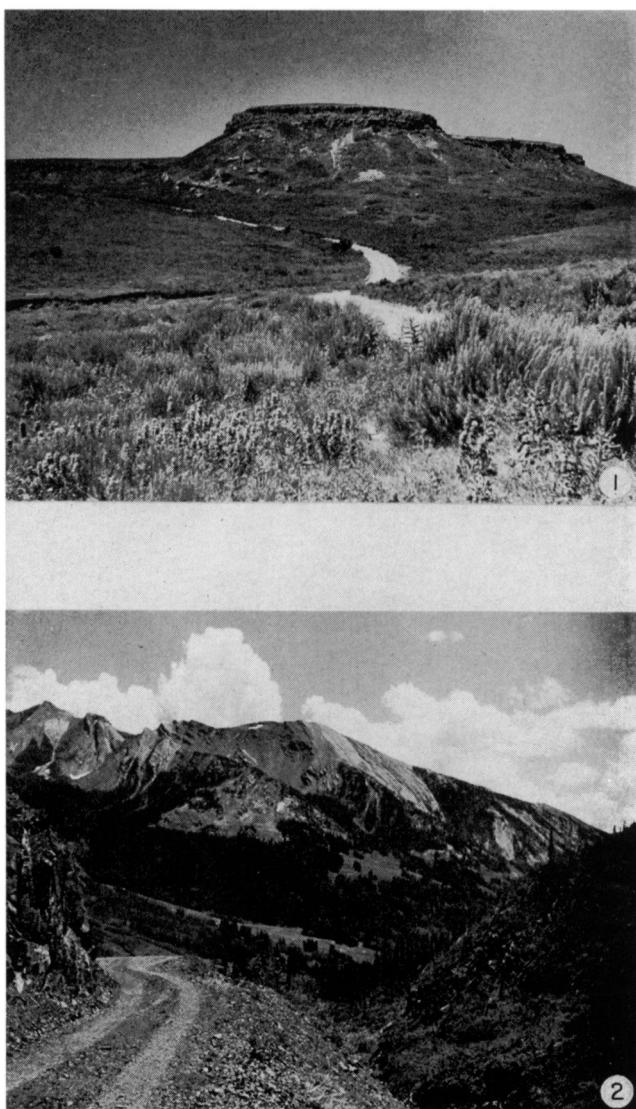


PLATE XIII. Habitats of *Townsendia*. Fig. 1. The Antelope Hills in Roger Mills County, Oklahoma. *Townsendia texensis* is an endemic of this area, restricted to limestones exposed by stream erosion of the deep, black soils of the high plains. Fig. 2. Near Gothic, Gunnison County, Colorado. Apomicts of the endemic *T. Rothrockii* grow under snowbanks in red, sandstone soils at the tops of these mountains. They flower as the snow melts off. Apomicts of *T. leptotes* are found at the mountain crests also, but on drier sites.

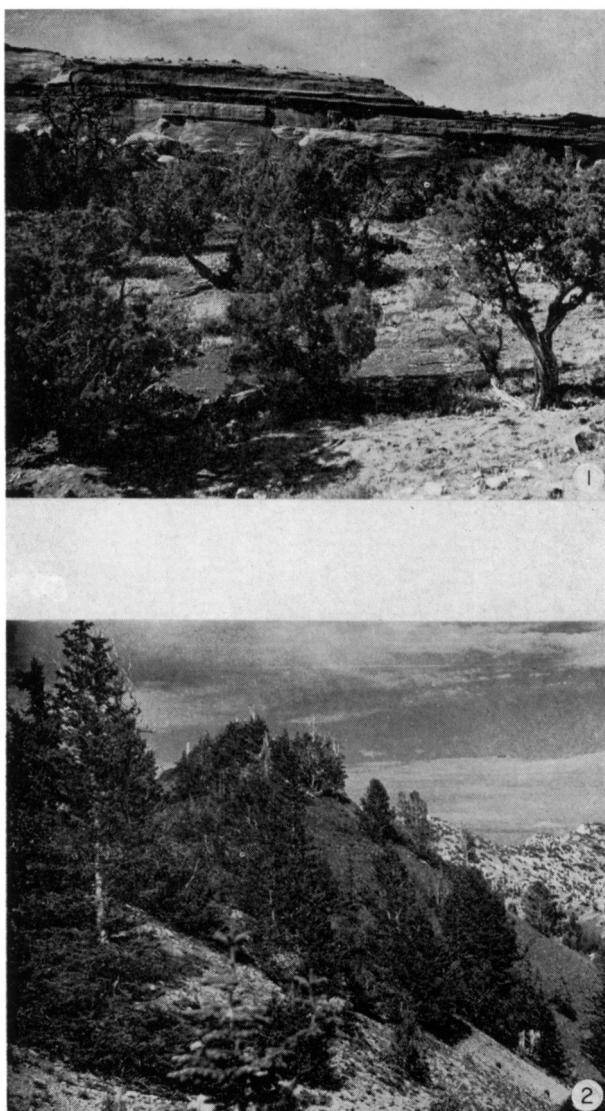


PLATE XIV. Habitats of *Townsendia*. Fig. 1. In the Colorado National Monument near Grand Junction, Mesa County, Colorado. A typical locality for *T. incana*. Both sexual and apomictic plants are found here. Fig. 2. The type-locality of *T. montana* var. *montana*, above the Flagstaff Mine at Alta, Salt Lake County, Utah. The plants are restricted to the crest of this subalpine limestone ridge.

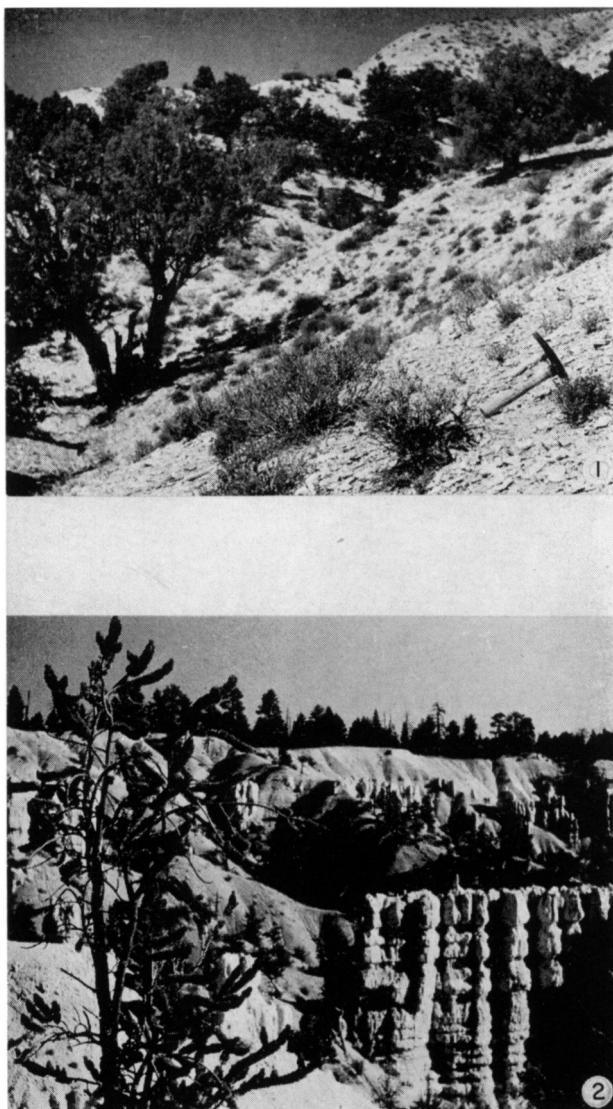


PLATE XV. Habitats of *Townsendia*. Fig. 1. A white shale outcrop of the Green River formation in the Uinta Basin of Utah. The endemic *T. mensana* var. *mensana* is found amidst the shale fragments. Fig. 2. Fairyland Canyon near Bryce Canyon in Garfield County, Utah. The endemic *T. montana* var. *minima* grows in finely-fragmented limestones at the tops of these cliffs.

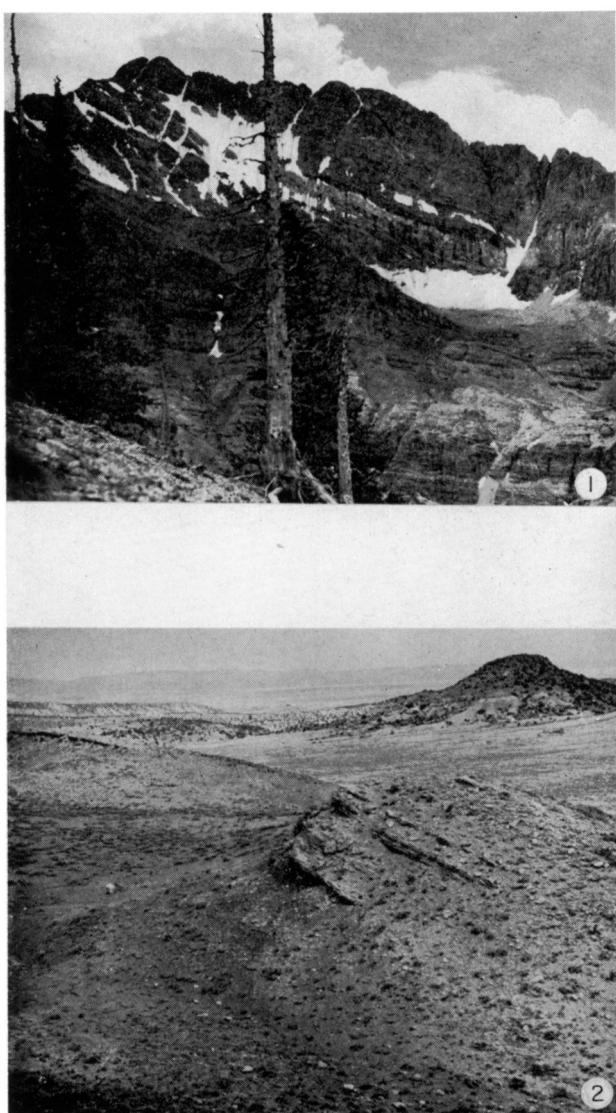


PLATE XVI. Mt. Borah, the highest peak in Idaho. Apomicts of *T. condensata*, *T. leptotes*, *T. montana* var. *montana* and *T. Parryi* grow on the limestones of this mountain. Fig. 2. The Satanka formation, near Alcova, Natrona County, Wyoming. Nuttall may have first collected *T. spathulata* here in 1834. The densely rosulate little plants of this species are abundant in localized areas among the shale fragments.

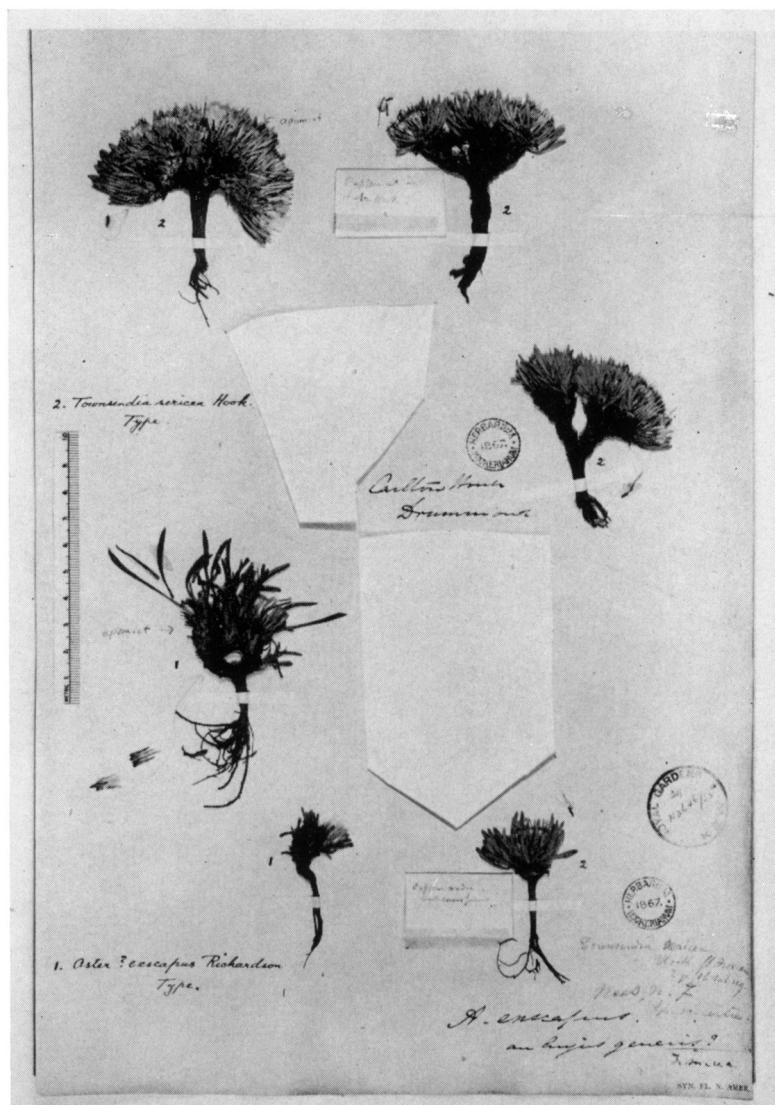


PLATE XVII. Photograph of the original collections of *Townsendia* (see explanation in the discussion of *T. exscapa*).

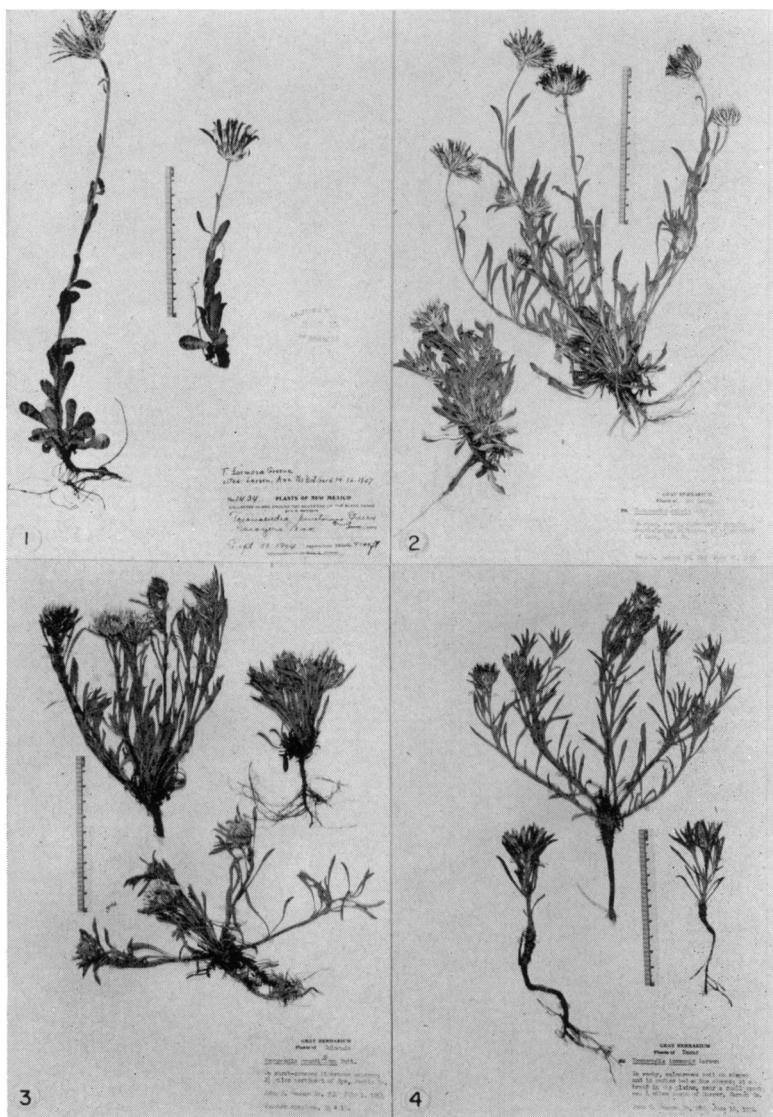


PLATE XVIII. Photographs of representative specimens of species of *Townsendia*.
Fig. 1. The lectotype of *T. formosa*. Fig. 2. A representative specimen of *T. eximia*.
Fig. 3. A representative specimen of *T. grandiflora*. Fig. 4. A representative specimen
of *T. texensis*.

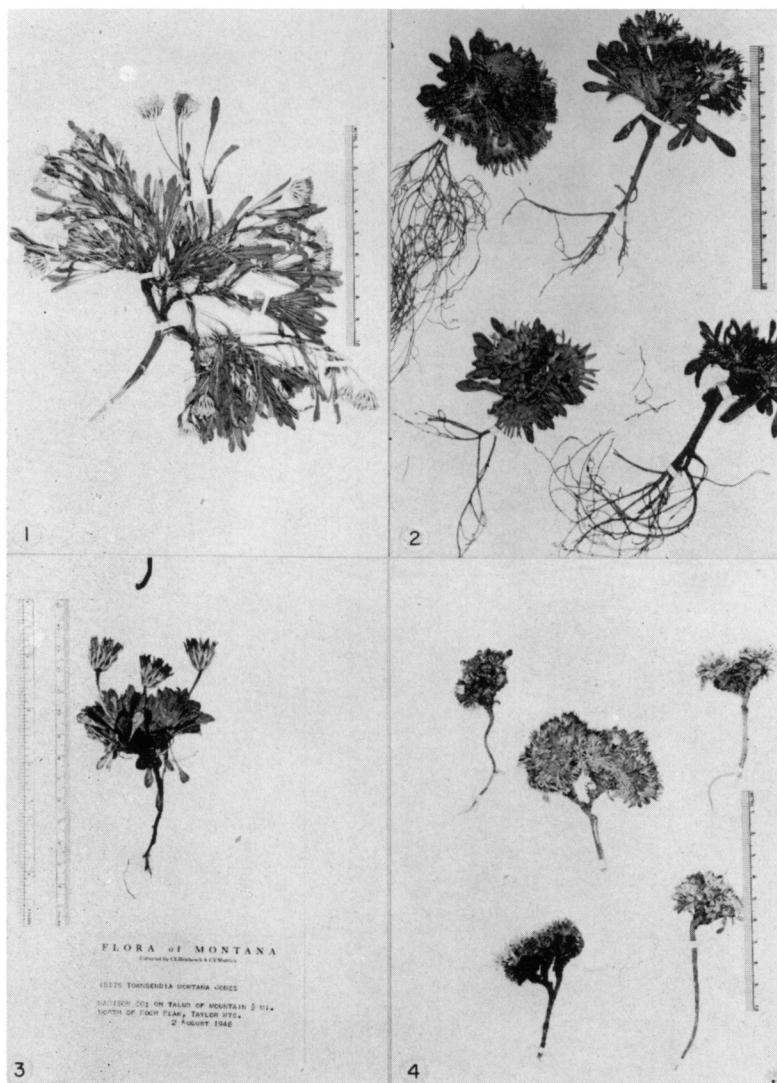


PLATE XIX. Photographs of representative specimens of *Townsendia*. Fig. 1. *Townsendia glabella* (Turner 2892). Fig. 2. *Townsendia Rothrockii* (Beaman, Weber, & Preece 514). Fig. 3. *Townsendia montana* var. *montana*. Fig. 4. *Townsendia montana* var. *minima* (Hitchcock 2962).

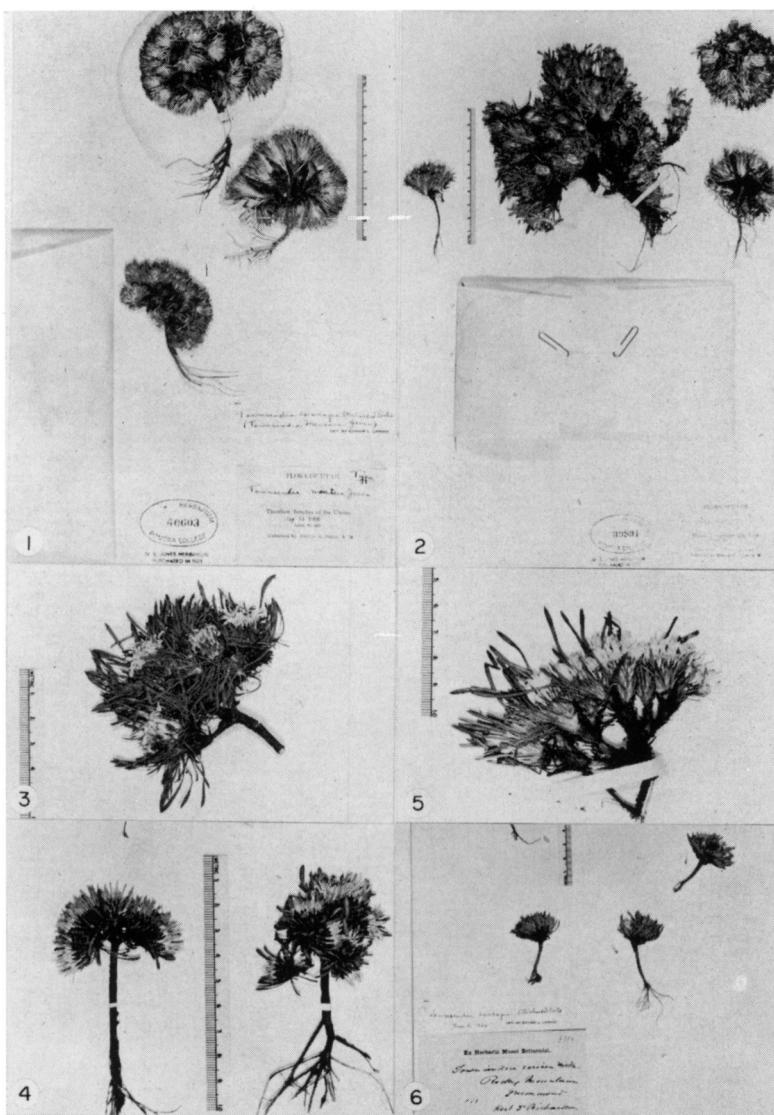


PLATE XX. Photographs of representative specimens of *Townsendia*. Fig. 1. The holotype of *T. mensana* var. *mensana*. Fig. 2. The holotype of *T. mensana* var. *Jonesii*. Fig. 3. A representative sexual specimen of *T. leptotes* (Ripley & Barneby 7589). Fig. 4. A representative apomictic specimen of *T. leptotes* (Holmgren & Shaw 7640). Fig. 5. The holotype of *T. Hookeri* (Clokey 4338, colo 12061). Fig. 6. Part of Drummond's collection (Drummond 573) of *T. Hookeri* from the Rocky Mountains.

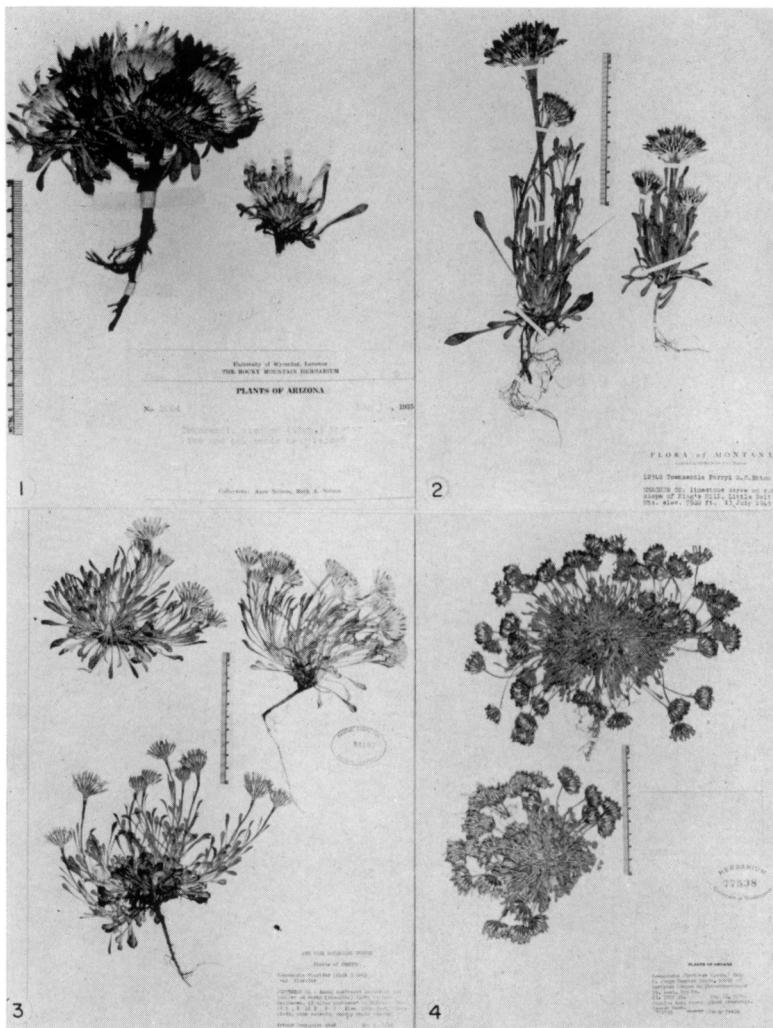


PLATE XXI. Photographs of representative specimens of species of *Townsendia*.
Fig. 1. *Townsendia escapa*. Fig. 2. *Townsendia Parryi*. Fig. 3. *Townsendia florifer*.
Fig. 4. *Townsendia scapigera*.

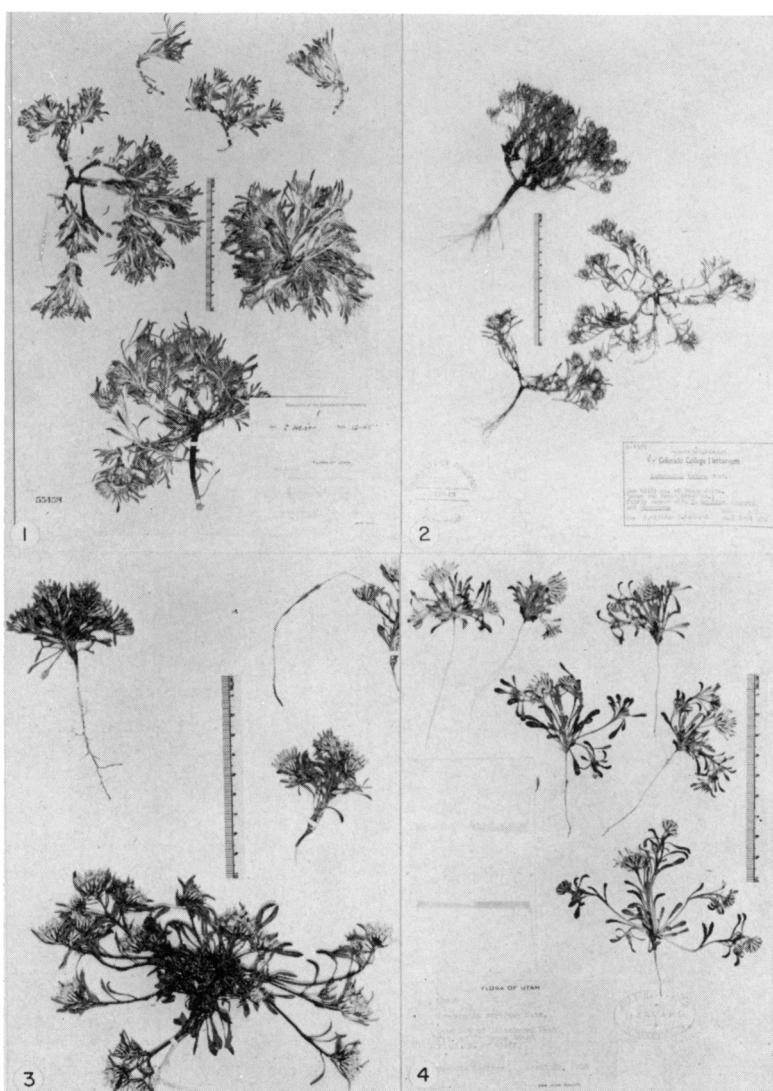


PLATE XXII. Photographs of representative specimens of species of *Townsendia*. Fig. 1. A representative specimen of *T. incana*. Fig. 2. A representative specimen of *T. Fendleri*. Fig. 3. A representative specimen of *T. strigosa* (Holmgren & Tillett 9474). Fig. 4. The holotype of *T. annua* (GH).

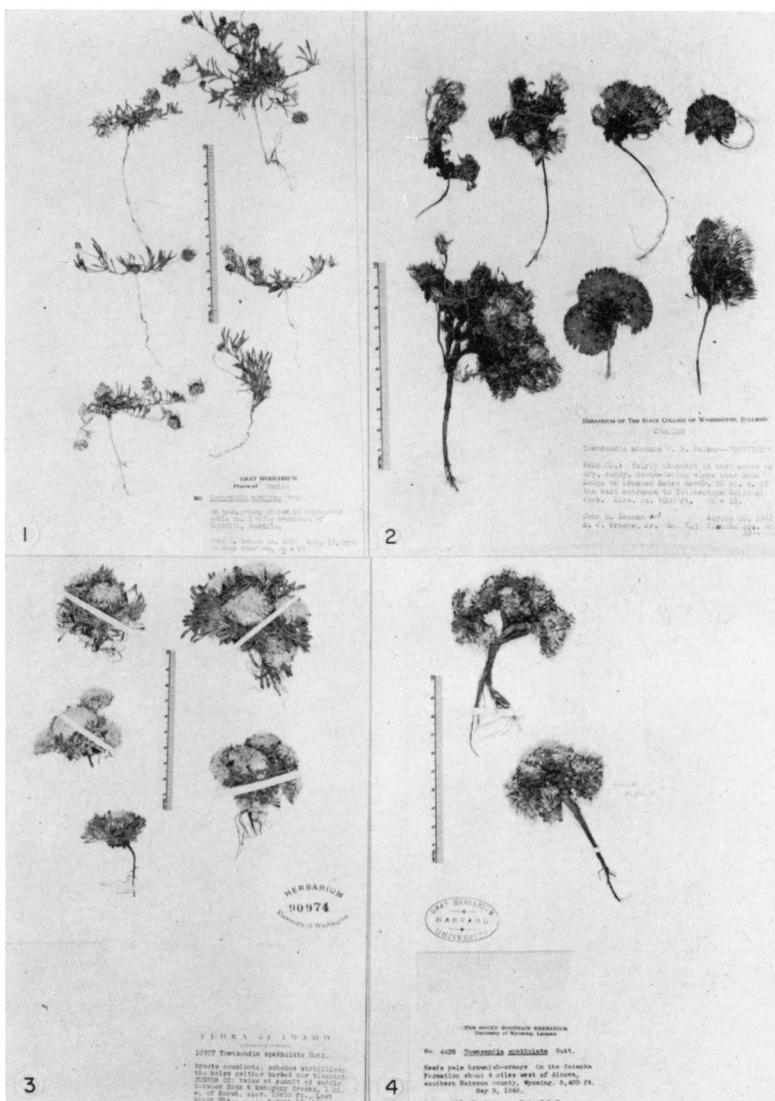


PLATE XXIII. Photographs of representative specimens of *Townsendia*. Fig. 1. *Townsendia mexicana*. Fig. 2. Sexual *T. condensata*. Fig. 3. Apomictic *T. condensata*. Fig. 4. *Townsendia spathulata*.

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