THE TAXONOMY OF THE GENUS ASTRANTHIUM (COMPOSITAE-ASTEREAE)

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Diederik Cornelis Dignus De Jong

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This is to certify that the

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Diederik Cornelis Dignus De Jong

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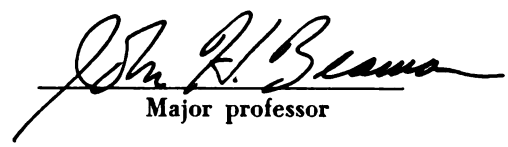

Major professor

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ABSTRACT

THE TAXONOMY OF THE GENUS
ASTRANTHIUM (COMPOSITAE-ASTEREAE)

by Diederik Cornelis Dignus De Jong

The genus Astranthium of the family Compositae, tribe Astereae, subtribe Asterinae, consists of perennial, biennial, and annual herbs indigenous to Mexico and the south-central and east-central United States. Ten species are now recognized, of which three have been newly described and one has been given a new name.

Most Mexican species are montane and occupy cool, moist, habitats at elevations between 1700 and 2900 meters. The most primitive species, A. xylopodum, is found on relatively dry sites in western Mexico at elevations between 800 and 1500 meters. The upper altitudinal limit of the genus is reached by A. Besmanii at alpine elevations of about 3700 meters on Cerro Potosi in the Sierra Madre Oriental. Of the two species in the United States, one, A. integrifolium, consists of two subspecies which hybridize in the zone of overlap. No species of Astranthium have been found to be sympatric and no natural interspecific hybrids are known.

Chromosome numbers are now available for all taxa of Astranthium. Of the ten species in the genus, five are diploid, three are tetraploid, one is hexaploid, and one is octoploid. Chromosome studies have indicated that the basic chromosome numbers of Astranthium are $x = 3$, 4, and 5. The species with chromosome numbers on a base of

$\underline{x}$ = 5 are the most primitive in the genus, those with $\underline{x}$ = 4 are intermediate in morphological characters, while those on $\underline{x}$ = 3 are the most advanced. Morphological, karyological, and anatomical evidence supports the postulate that a stepwise, aneuploid reduction in basic chromosome number has taken place in Astranthium. The reduction from $\underline{x}$ = 5 to $\underline{x}$ = 4 is inferred, but the $\underline{x}$ = 4 to $\underline{x}$ = 3 drop is supported by direct cytogenetic evidence obtained from experimental crosses.

Astranthium is thought to have originated in western Mexico during the Pliocene. It became more widespread during the Pleistocene in response to cooler climatic conditions which allowed populations to migrate along montane avenues of dispersal. Geographic isolation is thought to have been a major factor in speciation in the genus.

The closest generic relatives of Astranthium are Townsendia and Dichaetophora. The subtribal positions of the genera traditionally placed in the subtribe Bellidinae, Astranthium being among these, have been investigated. It is concluded on the basis of studies of herbarium specimens that the Bellidinae are a heterogeneous, artificial group, and evidence is presented for the placement of these genera in other subtribes of the Asteraae. Astranthium has been placed in the subtribe Asterinae near Townsendia and Dichaetophora.

Four taxa previously placed in Astranthium are excluded from the genus and are considered to be members of the genus Achaetogeron; the appropriate transfers have been made.

THE TAXONOMY OF THE GENUS ASTRANTHIUM (COMPOSITAE-ASTEREAE)

By

Diederik Cornelis Dignus De Jong

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I am also grateful to the curators of the herbaria from which specimens were borrowed. These herbaria are listed at the beginning of the systematic treatment.

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INTRODUCTION

Astranthium, a genus of the Compositae, tribe Astereae, subtribe Asterinae, is indigenous to Mexico and the south-central and east-central United States. The American species are well represented in the major herbaria, but a disproportionately small number of collections is available for the Mexican species.

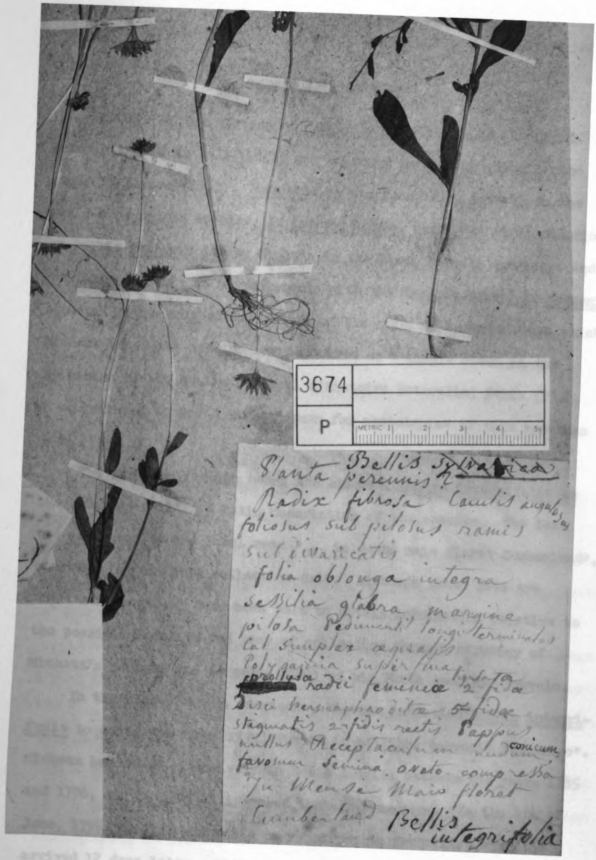
The genus has often been confused with other genera of the Astereae which it superficially resembles. Shinners (1946a) wrote: "The taxonomy of the Compositae has suffered greatly from the excessive reliance on the nature of the pappus, or its presence or absence, as a character of generic value". This factor has undoubtedly been responsible for much of the confusion in the taxonomy of Astranthium. On the basis of the reduced or absent pappus, Astranthium was long considered to be congeneric with the European Bellis. Also, Larsen (1933) in her monograph of Astranthium, used this character as the major generic criterion, placing in the genus species which had only the pappus character in common, but which differed greatly not only in other floral characters, but also in vegetative characters.

The present study was undertaken with the intention of attempting to clarify both intrageneric and intergeneric relationships. For this purpose, various biosystematic avenues were explored. Chromosome numbers, karyological data, crossing studies, and anatomical studies have been especially helpful in assessing phylogenetic relationships. In addition, an effort has been made to correlate the

possible evolution of *Astranthium* with climatic and orogenic events in the areas in which the genus occurs.

All taxa, except *A. robustum*, were studied in the field, but not all could be studied with the same intensity. Although I had at my disposal a considerably larger number of specimens than did Larsen (1933), and, in addition, benefitted from actual contact with the genus in the field, many problems need further exploration. It is hoped, however, that the present monograph will contribute to a better understanding of problems of classification in the Astereae.

Plate 1. Portion of the holotype (Michaux s. n., P) of Astranthium integrifolium (Michx.) Nutt., the type species of Astranthium. Reproduced from a Kodachrome slide taken by Dr. John H. Beaman at the Muséum National d'Histoire Naturelle, Paris.


3674
P
Bellis sylvestris Cyr.
Planta perennis
Radix fibrosa Caulis angulatus
foliosus sub pilosus rami
sub 2 varicati
folia oblonga integra
sessilia glabra margine
pilosa Pedunculi longi terminales
Cal simplex aequalis
Polygamia superflua
radii feminei
Disci hermaphroditi
stigmatis 2 fidi
nullus receptaculum conicum
favosum Semina oxato compressa
Ju Mense Maio floret
Cambridge
Bellis integrifolia

HISTORICAL ACCOUNT

Details of the history of Astranthium following its original description by Nuttall (1841) may be found in the monograph of the genus by Larsen (1933). Astranthium was founded by Nuttall on the basis of a single species, A. integrifolium, which was first described as Bellis integrifolia by Michaux in the Flora Boreali Americana and considered by him to be congeneric with the English Daisy, B. perennis. Apparently the only extant plants of the original material upon which Michaux based the species are contained on a single sheet in the Herbarium of the Muséum National d'Histoire Naturelle, Paris (P). I am indebted to Dr. John H. Beaman for photocopies of this specimen (see Plate 1).

The Paris collection bears the binomial Bellis integrifolia on the label as well as a Latin description of the species. The last two sentences on the label read "... in monte maio floret Cumberland", constituting the sole collection data. Although these data are admittedly vague, I have been able to obtain information relative to the possible locality and year of collection through scrutiny of Michaux's journal (in Sargent, 1889) of his North American travels.

In the Flora Boreali Americana, Michaux indicated Bellis integrifolia to occur "ad ripas rivulorum et in collibus umbrosis Tennassee". Michaux botanized extensively in North America between the years 1785 and 1796, and in 1795 he traveled through Tennessee. On the 4th of June, 1795, he left Knoxville on a journey to Nashville, where he arrived 12 days later. Although he crossed the Cumberland Mountains

and Cumberland River, it is most likely that the name "Cumberland" on the herbarium label refers to the environs of Nashville since he calls the city "la capitale des Etablissements de Cumberland". Following his arrival in Nashville, Michaux spent several days collecting plants and animals around the capital and it is most likely that he collected Bellis integrifolia at that time. That he collected the species in June, late in the flowering season, is borne out by the absence of the basal and lower cauline leaves and the fruiting condition of most of the heads. "In mense maio floret" undoubtedly refers merely to the month during which the species flowers most abundantly.

Collections of Bellis integrifolia were also made by Thomas Drummond and C. S. Rafinesque. Rafinesque (1837) considered Drummond's specimens from Texas, some of which apparently had been sent him by John Torrey, as distinct from B. integrifolia, and he described them as B. ciliata. In addition, Rafinesque described specimens from Kentucky and Tennessee as Bellis nutans and B. parviflora respectively, with several minor varieties. Velloso (1883) described three species of Bellis from Brazil, but his descriptions and illustrations show these species to be members of the Helianthese or Heleniese.

Nuttall, in his Genera of North American Plants (1818), recorded Bellis integrifolia as described by Michaux (1803) but suggested that the "... caulescent species ought probably to be separated". However, when Nuttall collected the species in 1819 along the banks of the Pottoe River (Nuttall's spelling) near Fort Smith, Arkansas, he noted in his diary (1821) "... the charming Daisey of America... altogether corresponding in general aspect with the European species..."

Subsequent study of Bellis integrifolia apparently convinced Nuttall that his original opinion on the status of the species was correct and in 1841 he segregated Astranthium from Bellis.

Although Nuttall considered the genus to be distinct, botanists such as Gray (1859), Chapman (1889), and Robinson and Fernald (1908) continued to place it in synonymy under Bellis and nearly a century elapsed before Astranthium was accepted in the first monographic treatment of the genus by Larsen (1933). She transferred most of the Mexican species thus far referred under Bellis to Astranthium and recognized seven species and four varieties. Of these species, five are retained in this paper. Three of her taxa, A. mexicanum, A. mexicanum var. chihuahuense, and A. mimum, as well as Blake's (1937) A. guatemalense are excluded from the genus for reasons discussed elsewhere. I agree with Shinners (1950) that Astranthium integrifolium var. rosulatum is a mere growth form of var. ciliatum and it is reduced to synonymy. I have followed Larsen in recognizing Rafinesque's Bellis ciliata as an infraspecific taxon of Astranthium integrifolium; it is here treated as a subspecies rather than as a variety. Other taxa described by Rafinesque (1837) are considered to be synonymous with A. integrifolium subsp. integrifolium. A variety of A. integrifolium, var. robustum, described by Shinners (1950) from Trans-Pecos Texas, is here elevated to specific rank. The present monograph recognizes ten species, three of which are described for the first time. In addition the little known Chrysanthemum mexicanum H.B.K. has been found to be an Astranthium, but the combination A. mexicanum has already been used for a different species, and it is thus given a new name.

MATERIALS AND METHODS

Bud material for the study of chromosome numbers and meiotic chromosome configurations was collected in the field during the summer of 1960 and the spring and summer of 1961. The buds were placed in vials containing a freshly mixed Carnoy solution of 6 parts 95 per cent ethyl alcohol, 3 parts chloroform, and 1 part glacial acetic acid. The bud collections obtained in 1960 and in the spring of 1961 were refrigerated at 1° C upon return to East Lansing, but the buds collected in the summer of 1961 were kept refrigerated throughout the entire field trip, as outlined by De Jong and Longpre (1963). Slides were made by the aceto-carmine smear technique. Chromosomes were drawn with the aid of a Zeiss drawing apparatus under phase-contrast at an initial magnification of about 4000 diameters. Voucher specimens have been deposited in the Michigan State University Herbarium.

For karyotype studies, root tips were collected from plants grown in the greenhouse from field-collected seeds. The root tips were pretreated for one hour in a saturated solution of paradichlorobenzene, and fixed in a Carnoy solution of 3 parts 95 per cent ethyl alcohol and 1 part glacial acetic acid for 30 minutes. They were subsequently hydrolyzed in 1 N HCl at 60° C for three to five minutes and transferred to Feulgen for staining for a period of 30 minutes to two hours. Root tip squashes were made according to the standard procedure. The chromosomes stained darkly and were well spaced apart for optimum observation. From 3 to 12 ideograms were made of the karyotype of each species, and an average, representative karyotype was selected

on the basis of measurements with a millimeter rule.

Experimental crosses were carried out with greenhouse-grown plants. The plants were first checked for self-compatibility. Young heads were bagged and allowed to anthese. Anthesed heads were either left bagged or the heads of a plant were rubbed together at least half a dozen times and rebagged after each transfer of pollen. In both cases, seed set was observed and this was taken as an indication that the plants were self-compatible. On this basis, only the pistillate florets could be used for crossing purposes. Pre-anthesis disk florets were removed from the receptacle with fine tweezers and the heads, with only the ray florets left, were then bagged to prevent contamination. Each head contained from 15 to 35 ray florets, depending upon the species. When the stigmas were receptive, pollen was transferred by rubbing intact heads with anthesed disk florets, which had been bagged before anthesis, onto the stigmas. This procedure was repeated at least half a dozen times for each head during the ensuing three of four days. Following each transfer of pollen, the "female" heads as well as the heads of the "male" parent were carefully rebagged. Each cross was attempted with several plants, but the exact number of plants utilized was not recorded.

For the study of the vasculation of the ray and disk florets, both fresh and dried plants were used. Fresh material was placed in FAA for killing and fixing, washed in water, and transferred to 2.5 per cent aqueous NaOH for clearing. Dried material was placed directly in this clearing solution. Glacial acetic acid was used for terminal clearing, after which the florets were washed and dehydrated in an ethyl alcohol series. Whole mounts were prepared by removing cleared

material to a 1 per cent solution of safranin in equal parts of absolute ethyl alcohol and xylene for staining, after which the florets were transferred to xylene and mounted in balsam.

Fresh and dried heads were used for histological studies. Fresh material was killed and fixed in FAA and dried material was softened and cleared as above. The heads were then washed and infiltrated and embedded according to the tertiary butyl alcohol method of Johansen (1940). Staining was carried out with safranin and fast green according to Northen's variation of Foster's tannic acid-ferric chloride method (Johansen, 1940).

Table 1. Meiotic chromosome numbers in *Astranthium*.

taxon	n number	collection or reference
A. xylopodum	5	De Jong and Longpre (1963)
A. laetificum	10	MICHOACAN: 1.5 mi W of Mil Cumbres, *De Jong 1104*
A. purpurascens	8	Turner, Beaman, and Rock (1961); De Jong and Longpre (1963)
	8	CHIAPAS: ca 5 mi E of San Cristobal de Las Casas, *King 2803*, Turner, Ellison, and King (unpubl.)
	8	CHIAPAS: just W of San Cristobal de Las Casas, *King 2996*, Turner, Ellison and King (unpubl.)
	8 + 1 or 2 fragments	CHIAPAS: ca 10 mi E of Teopisca, *King 3011*, Turner, Ellison, and King (unpubl.)
	8	CHIAPAS: 9 mi NW of Comitan, *De Jong 1146*
	8	CHIAPAS: 5.2 mi E of Teopisca, *De Jong 1164*
	8	OAXACA: between KMs 412 and 413, Route 190, *De Jong 1131*
	8	OAXACA: 0.2 mi W of El Fortin, Route 190, *De Jong 1176*
A. xanthocomoides	8	Turner, Beaman, and Rock (1961); De Jong and Longpre (1963)
A. integrifolium subsp. *integrifolium*	4	Baldwin (1941, reported as *A. integrifolium*)

Table 1 - Continued

taxon	n number	collection or reference
A. integrifolium subsp. integrifolium	4	TENNESSEE: Davidson County, ca 20 mi S of Nashville, Channell 8880
A. integrifolium subsp. ciliatum	4	OKLAHOMA: Pittsburg County, 2 mi N of Crowder, De Jong 770
	4	OKLAHOMA: Pittsburg County, 6.5 mi E of Arpellar, De Jong 783
	4	OKLAHOMA: Hughes County, 4.7 mi E of Pontotoc County line, De Jong 789
	4	TEXAS: Colorado County, 8 mi NW of Eagle Lake, Turner 4350, Turner (unpubl.)
	4	TEXAS: San Patricio County, 6 mi NE of Sinton, Turner 4466, Turner (unpubl.)
A. splendens	9	NUEVO LEON: between KMs 30 and 31, road to Dr. Arroyo, De Jong 1240
	9	NUEVO LEON: between KMs 29 and 30, road to Dr. Arroyo, De Jong 1244
A. Beamanii	12	Turner, Beaman, and Rock (1961, reported as Astranthium sp.)
	12	NUEVO LEON: SE slope of Cerro Potosi, De Jong 504
	12	NUEVO LEON: alpine meadow, peak of Cerro Potosi, De Jong 509
	12	NUEVO LEON: N side of peak, Cerro Potosi, De Jong 510
	12	NUEVO LEON: alpine meadow, peak of Cerro Potosi, De Jong 766
	12	E slope of Cerro Potosi, De Jong 769

Table 1 - Continued

taxon	n number	collection or reference
A. orthopodum	3	De Jong and Longpre (1963)
	3	DURANGO: ca 31 mi SW of Ciudad Durango, King 3744, Turner, Ellison, and King (unpubl.)
A. condimentum	3	JALISCO: 35 mi SW of Jiquilpan, De Jong 1027
	3	MICHOACAN: ca 33 mi W of Morelia, King 3631, Turner, Ellison, and King (unpubl.)
	3	MICHOACAN: at KM 43.5, Route 39 from Carapan to Uruapan, De Jong 760
	3	MICHOACAN: 4 mi S of Villa Escalente, De Jong 1082
	3	MICHOACAN: 5.4 mi E of Quiroga, De Jong 1091
A. robustum	3	TEXAS: Golf Course, Alpine, Warnock s.n.

Plate 2. Fig. 1 - 11. Meiotic chromosomes of *Astranthium*, X 1470. Fig. 1. *A. xylopodum*, *n* = 5 (*De Jong* 1028). Fig. 2. *A. laetificum*, *n* = 10 (*De Jong* 1104). Fig. 3. *A. purpurascens*, *n* = 8 (*De Jong* 1227). Fig. 4. *A. xanthocomoides*, *n* = 8 (*De Jong* 1195). Fig. 5. *A. integrifolium* subsp. *integrifolium*, *n* = 4 (*Channell* 8880). Fig. 6 *A. integrifolium* subsp. *ciliatum*, *n* = 4 (*De Jong* 789). Fig. 7. *A. splendens*, *n* = 9 (*De Jong* 1244). Fig. 8. *A. Beamanii*, *n* = 12 (*De Jong* 769). Fig. 9. *A. orthopodum*, *n* = 3 (*De Jong* 784). Fig. 10. *A. condimentum*, *n* = 3 (*De Jong* 1080). Fig. 11. *A. robustum*, *n* = 3 (*Warnock* s.n.).

CYTOLOGICAL INVESTIGATIONS

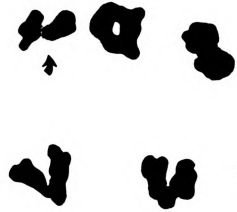
A. Chromosome Numbers.

Chromosome numbers determined from observations of pollen mother cells are listed in Table 1 (cf. also Plate 2). Meiosis was regular in all taxa examined except in one population of Astranthium integrifolium (De Jong 790) from Fayetteville, Arkansas. This population was morphologically intermediate between subspp. integrifolium and ciliatum. Twenty rosettes of the population were collected in the field in the spring of 1961 and grown to maturity in the greenhouse. All plants were examined cytologically: 18 plants had $n = 4$ while two had $n = 5$ (cf. Plate 3, Fig 1 - 6). In these two plants the fifth chromosome sometimes appeared as a small bivalent with normal anaphase movement, but in other instances it was found attached by slender chromatin threads to another chromosome. Root tips of the two plants all had ten chromosomes, the extra pair evident as small chromosomes with subterminal centromeres. One possible explanation is that the $n = 5$ plants resulted from an aneuploid increase following a series of unequal translocations. In view of the presence in Astranthium of the basic number $x = 5$, another possibility is that they are survivors of an ancestral form with $n = 5$. The two plants could not be distinguished morphologically from those with $n = 4$.

The occurrence of the basic chromosome numbers $x = 5$, 4, and 3, suggests that a stepwise, aneuploid reduction of the basic chromosome number of the "Crepis" type (Babcock, 1942) has taken place in

Plate 3. Fig. 1 - 6. Meiotic and mitotic configurations in *Astranthium integrifolium* (De Jong 790), X 4000. Fig. 1. Normal chromosome number, $n = 4$, metaphase, I. Fig. 2. Diakinesis, $n = 5$, extra bivalent indicated by arrow. Fig. 3. Diakinesis, $n = 5$, extra chromosome (arrow) attached by chromatin threads. Fig. 4. Diakinesis, $n = 5$, extra bivalent shown by arrow; hatched area lightly stained. Fig. 5 and 6. Somatic metaphase, $2n = 10$, extra pair shown by arrows in Fig. 5.

1



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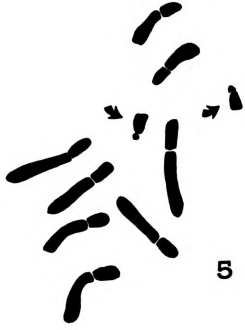
3

4



5

6

Astranthium. Although evidence for the drop from $\underline{x} = 5$ to $\underline{x} = 4$ can only be inferred at the present time, direct cytogenetic evidence for the drop from $\underline{x} = 4$ to $\underline{x} = 3$ has been obtained. As indicated in the section on experimental crosses, F_1 hybrids obtained from a cross between A. integrifolium subsp. integrifolium ($\underline{n} = 4$) and A. condimentum ($\underline{n} = 3$) showed one trivalent and two bivalents at diakinesis of microsporogenesis (Plate 6, Fig. 1 - 5), indicating homology between the four chromosomes of the one parent with the three of the other. In addition, F_1 hybrids obtained from crosses between other members with chromosome numbers based on $\underline{x} = 4$ and $\underline{x} = 3$ showed a high percentage of trivalent formation. This the second time that evidence for aneuploid reduction has been directly observed in a genus of the Asteraceae. Jackson (1962) found a similar case in Haplopappus sect. Blepharodon.

Five species of Astranthium are diploid and the other five, all Mexican, are polyploid. Of these polyploids, three are tetraploid, one is hexaploid, and one is octoploid. It may be inferred from the regular pairing configurations of the polyploids that they are allopolyploids. All polyploids are perennials.

B. Karyotype Studies.

Huziwara (1959, and papers cited therein) has conducted a number of karyotype investigations in the Asteraceae, subtribe Asterinae. The results of his studies have been of considerable value in determining phylogenetic trends. The diverse array of chromosome numbers in Astranthium prompted me to undertake a survey of karyotypes in all taxa in order to determine whether or not evolution of chromosome morphology

Table 2. Measurements of the somatic chromosomes of taxa of *Astranthium*.

taxon	chromosome pairs	length in microns	short arm length/total length (X100)	position of centromere
A. xylopodum	1, 2	9.0	50	submedian
	3, 4	8.2	42	submedian
	5, 6	8.0	40	submedian
	7, 8	5.0	40	submedian
	9, 10	4.0	30	submedian
A. laetificum	1, 2	7.0	50	median
	3, 4	7.0	40	submedian
	5, 6	6.2	50	median
	7, 8	4.9	25	subterminal
	9, 10	4.3	35	submedian
	11, 12	4.2	33	submedian
	13, 14	4.0	38	submedian
	15, 16	3.4	41	submedian
	17, 18	3.0	33	submedian
	19, 20	2.3	35	submedian
A. purpurascens	1, 2	5.5	43	submedian
	3, 4	4.3	23	subterminal
	5, 6	4.0	38	submedian
	7, 8	3.8	26	subterminal
	9, 10	3.8	26	subterminal
	11, 12	3.4	30	submedian
	13, 14	3.1	26	subterminal
	15, 16	1.5	27	subterminal
A. xanthocomoides	1, 2	4.1	32	submedian
	3, 4	3.4	28	subterminal
	5, 6	3.1	26	subterminal
	7, 8	3.0	33	submedian
	9, 10	2.8	35	submedian
	11, 12	2.4	38	submedian
	13, 14	1.9	47	submedian
	15, 16	1.4	21	subterminal

Table 2 - Continued

taxon	chromosome pairs	length in microns	short arm length/total length (X100)	position of centromere
A. integrifolium subsp. integrifolium	1, 2	4.8	36	submedian
	3, 4	3.8	29	subterminal
	5, 6	3.3	33	submedian
	7, 8	3.0	33	submedian
A. integrifolium subsp. ciliatum	1, 2	4.3	33	submedian
	3, 4	3.8	29	subterminal
	5, 6	3.1	32	submedian
	7, 8	2.8	32	submedian
A. splendens	1, 2	4.8	48	submedian
	3, 4	4.6	28	subterminal
	5, 6	3.7	24	subterminal
	7, 8	3.6	27	subterminal
	9, 10	3.5	28	subterminal
	11, 12	3.3	33	submedian
	13, 14	3.1	26	subterminal
	15, 16	3.1	26	subterminal
	17, 18	2.8	28	subterminal
A. Beesandii	1, 2	4.4	37	submedian
	3, 4	4.3	23	subterminal
	5, 6	4.3	43	submedian
	7, 8	3.6	31	submedian
	9, 10	3.5	28	subterminal
	11, 12	3.3	33	submedian
	13, 14	3.2	28	subterminal
	15, 16	2.9	27	subterminal
	17, 18	2.8	20	subterminal
	19, 20	2.8	35	submedian
	21, 22	2.6	31	submedian
	23, 24	2.6	31	submedian
A. orthopodum	1, 2	3.8	26	subterminal
	3, 4	3.6	22	subterminal
	5, 6	2.9	31	submedian
A. condimentum	1, 2	4.0	25	subterminal
	3, 4	3.8	26	subterminal
	5, 6	3.3	33	submedian

Table 2 - Continued

taxon	chromosome pairs	length in microns	short arm length/total length (X100)	position of centromere
A. robustum	1, 2	4.1	31	submedian
	3, 4	3.8	21	subterminal
	5, 6	3.2	27	subterminal

paralleled that of gross morphological and anatomical characters. Procedures have been outlined in the section on materials and methods. The measurements of the chromosomes of each taxon are listed in Table 2 and ideograms for all taxa are shown on Plate 4.

Observations.

1. Astranthium xylopodum ($2n = 10$).

This species is diploid on a base of $x = 5$ and has the largest chromosomes of any species in the genus. Chromosome size ranges from 4.0 - 9.0 microns. Of the five pairs, four have submedian centromeres, whereas the largest pair has median centromeres. The smallest pair bears satellites.

2. Astranthium laetificum ($2n = 20$).

The karyotype of this tetraploid species is characterized by a predominance of chromosomes with submedian centromeres. Two pairs have median centromeres and only one pair has subterminal centromeres. The second smallest pair has satellites. Total chromosome length ranges from 2.3 - 7.0 microns.

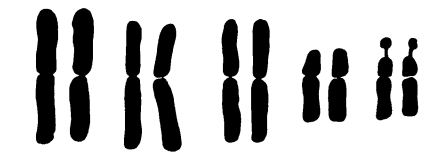
3. Astranthium purpurascens ($2n = 16$).

This species is tetraploid on a base of $x = 4$. Of the eight pairs of chromosomes in the complement, three pairs have submedian centromeres, the remaining pairs have subterminal centromeres. Total chromosome length ranges from 1.5 microns to 5.5 microns. The smallest pair has satellites.

4. Astranthium xanthocomoides ($2n = 16$).

In this tetraploid species, five pairs have submedian centromeres,

Plate 4. The karyotypes of the taxa of Astranthium. The chromosomes are arranged according to decreasing total length. The species sequence corresponds to that of the systematic treatment.



A. XYLOPODUM

A. LAETIFICUM

A. PURPURASCENS

A. XANTHOCOMOIDES

A. INTEGRIFOLIUM subsp. INTEGRIFOLIUM

A. INTEGRIFOLIUM subsp. CILIATUM

A. SPLENDENS

A. BEAMANII

A. ORTHOPODUM

A. CONDIMENTUM

A. ROBUSTUM

while three pairs have subterminal centromeres. As in A. purpurascens, the smallest pair has satellites. Chromosome size ranges from 1.4 to 4.1 microns.

5. Astranthium integrifolium subsp. integrifolium (2n = 8).

The majority of the preparations which I made of the root tips showed the largest pair of chromosomes with extremely small satellites. In certain instances, however, these were not visible and must have been obscured by the short arm of the chromosomes. Chromosome size ranges from 3.0 to 4.8 microns. Three pairs have submedian centromeres, while only one pair has subterminal centromeres.

6. Astranthium integrifolium subsp. ciliatum (2n = 8).

The somatic chromosomes of subsp. ciliatum are slightly smaller than those of subsp. integrifolium. This is also reflected in the size of the pollen grains of the two taxa. In subsp. integrifolium, pollen grain size ranges from 16.0 to 20.0 microns, with an average of 17.5 microns; subsp. ciliatum has pollen grains with a size range of 15.0 to 18.0 microns, averaging 16.5 microns. The largest chromosome pair in this subspecies also has small satellites.

7. Astranthium splendens (2n = 18).

This species is hexaploid on a base of x = 3. Of the nine pairs in the complement, seven pairs have subterminal centromeres, the remaining pairs submedian centromeres. Two pairs of satellited chromosomes are present. Chromosome size ranges from 2.8 to 4.8 microns.

8. Astranthium Besseranii (2n = 24).

This octoploid species has chromosomes which range from 2.6 to

4.4 microns in length. Five pairs have subterminal centromeres, whereas seven pairs have submedian ones. As in A. splendens, the karyotype of A. Beamanii has two pairs of satellited chromosomes.

9. Astranthium orthopodum ($2n = 6$).

A. orthopodum is diploid with 6 somatic chromosomes, four of which have subterminal centromeres. The smallest pair has submedian centromeres and is 2.9 microns long. The largest pair, which bears satellites, is 3.8 microns in length.

10. Astranthium condimentum ($2n = 6$).

The six chromosomes of this diploid species range from 3.3 to 4.0 microns. As in A. orthopodum, the smallest pair has submedian centromeres, the remaining pairs have subterminal centromeres. The largest pair consists of satellited chromosomes.

11. Astranthium robustum ($2n = 6$).

As in A. orthopodum and A. condimentum, the largest chromosome pair has satellites, but the centromeres are submedian rather than subterminal. The smaller pairs have subterminal centromeres. Chromosome length ranges from 3.2 to 4.1 microns.

C. Discussion.

Chromosome number, size, position of the centromere, and presence of secondary constrictions have proven useful as karyotype characters in Astranthium. The chromosome complements of A. xylopodum ($2n = 10$) and A. laetificum ($2n = 20$) contain the largest chromosomes of any species in the genus. In addition, their karyotypes are largely symmetrical, i.e., there is a preponderance of chromosomes

with median centromeres and submedian centromeres, while chromosomes with subterminal centromeres are absent or few. This condition is generally considered to be primitive (cf. Stebbins, 1950) and is in agreement with the cytogenetic evidence which suggests that the basic chromosome numbers $\underline{x} = 4$ and $\underline{x} = 3$ have been derived through aneuploid loss. The species which have chromosome numbers on a base of $\underline{x} = 4$, and which are intermediate in morphological characters, also have intermediate karyotypes. The species with $\underline{x} = 3$, which are morphologically specialized, have karyotypes which are asymmetrical with a predominance of subterminal centromeres. These species also have smaller chromosomes than the primitive species.

The karyotypes of A. xylopodum and A. laetificum show many similarities in chromosome size and position of centromeres. There is a sharp break in total chromosome length between the third and fourth pair in A. xylopodum and in short-arm length between the third and fourth pair of A. laetificum. In contrast, the somatic chromosomes of all other taxa, when arranged according to decreasing length, show a graded series. Astranthium xylopodum and A. laetificum are also more sharply differentiated from the rest of the genus by gross morphological characters than are any other species. It is perhaps also significant in this respect that attempts to produce hybrids between A. laetificum and species with $\underline{x} = 4$ and $\underline{x} = 3$ (especially A. purpurascens with $\underline{n} = 8$, A. splendens with $\underline{n} = 9$, and A. Beaumii with $\underline{n} = 12$) failed, while hybrids could be synthesized between species with $\underline{x} = 4$ and $\underline{x} = 3$.

Species which are related morphologically and which have the same chromosome number often have secondary constrictions on the same

chromosome pairs. This is especially striking in A. purpurascens and A. xanthocomoides in which the smallest pair bears satellites, and in A. orthopodum, A. condimentum, and A. robustum, in which the largest pair has secondary constrictions. Astranthium splendens and A. Beamanii have satellites on the second and fourth chromosome pairs. The karyotypic data are especially important in connection with these two species in supporting the assumption that their basic chromosome number is $x = 3$ (cf. also discussion under A. splendens). Although $x = 9$ has been shown by Solbrig et al. (1964) to be the most common basic number in the Asteraae, the occurrence of $n = 12$ in A. Beamanii makes it appear unlikely that $n = 9$ is a diploid number in the morphologically very similar A. splendens. It is more likely that A. splendens is a hexaploid on a base of $x = 3$, and this hypothesis is supported by its advanced karyotype morphology as compared to that of other species of Astranthium.

Two independent, opposing trends in chromosome evolution have occurred in Astranthium, and both trends seem to provide definite selective advantages. On the one hand, there has been a reduction of the basic chromosome number through aneuploid loss, and on the other, an increase in chromosome number through polyploidy. The two species with the basic number $x = 5$ are primitive perennials; one is diploid, the other tetraploid. Two polyploid species with $x = 4$ are perennial, as are a hexaploid and an octoploid species on the base of $x = 3$. Since these species are primarily montane, it is possible that both the perennial habit and polyploidy may have a selective advantage for plants occupying cool, moist habitats in the mountains. It is perhaps significant in this respect that the highest polyploid, A. Beamanii,

occurs at higher elevations than any other species of the genus. A correlation of the perennial habit and polyploidy with high elevations and latitudes is well known (Gustafsson, 1948). The reasons for this phenomenon are not yet entirely clear, however.

In contrast to the occurrence of polyploids in montane areas, two of the more advanced, diploid species, A. integrifolium and A. robustum, are annuals and are found in warmer, drier habitats at lower elevations. Two other advanced species, A. orthopodum and A. condimentum, occur in mountainous areas, but their habitats may be specialized in some other way, as is suggested by their restricted geographical distribution.

Relatively minor climatic changes may have had significant effects on the habitats which the species with low numbers occupy. The ability to evolve adaptations to new environmental conditions would be important to their survival. This would seem to be especially important with respect to the supposed Pleistocene evolution of the genus (see under Origin). The rapid expression of genes or gene combinations might be facilitated by the low chromosome numbers. The annual habit of these species, which would necessitate segregation and recombination every year, may also have been important in increasing their potential for rapid evolutionary change. Solbrig et al. (1964) have found that genera of the Asteraeae with low chromosome numbers are especially frequent in arid areas of the Southwest and Mexico. They also believe that these low numbers may represent adaptations to specialized habitats.

Morphological and physiological changes in the species of Astranthium may have been accompanied by and possibly, but not

necessarily, facilitated by changes in the karyotype. Progressive changes from symmetrical to asymmetrical karyotypes and from large to medium-sized to small chromosomes probably resulted from translocations and inversions. Perhaps it is the new gene combinations which result from these chromosomal alterations, rather than actual morphological changes in the karyotype itself, which have a selective advantage. The alteration of the karyotype may thus reflect only the fact that a greater number of translocations and inversions have occurred in taxa with an asymmetrical karyotype than in those in which it is symmetrical.

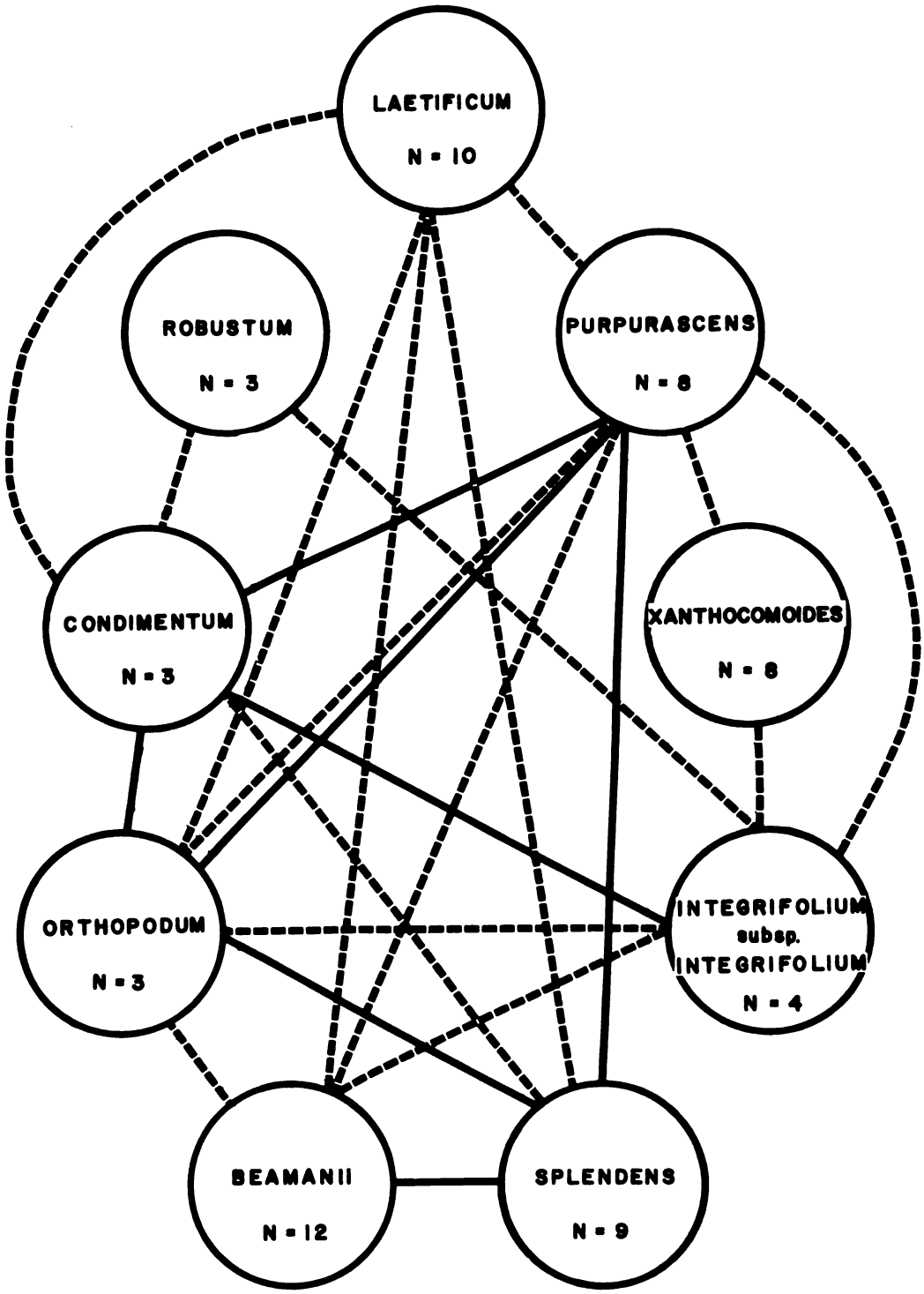
CROSSING STUDIES

Experimental crosses were attempted using greenhouse-grown plants of nine species of Astranthium. The crosses attempted are shown on Plate 5. Solid lines indicate successful crosses, broken lines unsuccessful crosses. Crossing procedures are outlined in the section on materials and methods.

The hybrid nature of the F_1 plants obtained was verified using the following criteria: (1) Their morphology was carefully compared with that of the parental species. In most instances, the hybrids were intermediate between the parents in quantitative characters, while qualitative characters such as ray color were found to be dominant. (2) The somatic chromosome number of each hybrid was checked while the plants were still in the vegetative stage. This was the most conclusive evidence for hybrids obtained from crosses between heteroploid parents. (3) Meiotic irregularities may be an indication of hybridity in hybrids whose parents show regular meiotic configurations. (4) The percentage pollen stainability of each hybrid was always considerably lower than that of either parent. On the basis of these criteria, there was never any doubt about the hybrid nature of the F_1 plants.

The parents which were used in the successful crosses and for which percentages of pollen stainability are known are listed in tabular form below.

Plate 5. Chart showing the experimental crosses carried out in greenhouse cultures of Astranthium. Solid lines indicate successful crosses, broken lines unsuccessful crosses. The haploid chromosome number of each taxon is indicated.


LAETIFICUM
N = 10
ROBUSTUM
N = 3
PURPURASCENS
N = 8
CONDIMENTUM
N = 3
XANTHOCOMOIDES
N = 8
ORTHOPODUM
N = 3
INTEGRIFOLIUM
subsp.
INTEGRIFOLIUM
N = 4
BEAMANII
N = 12
SPLENDENS
N = 9

species	collection	% pollen stainability
A. Beamanii	De Jong 766	99.8
A. condimentum	De Jong 760	90.0
A. orthopodum	De Jong 984	94.6
A. purpurascens	De Jong 1131	96.8
A. purpurascens	De Jong 1144	97.1
A. purpurascens	De Jong 1227	74.3
A. splendens	De Jong 1244	95.4

Observations on meiosis in the hybrids were made on pollen mother cells stained with aceto-carmine and observed on slides made according to the routine squash technique. The percentages of pollen stainability are based on a total of 1500 to 2000 grains from one to several heads from plants in culture. Pollen grains were stained with cotton-blue in lactophenol for a minimum of twelve hours. The percentages are based upon the number of grains which stained dark blue.

The hybridizations are grouped into two categories: (1) crosses between morphologically distinct, closely or more distantly related heteroploid or homoploid taxa, and (2) intraspecific crosses. Time was not available for crosses beyond the F_1 generation. The crosses in which F_1 hybrids were obtained are discussed below; the pollen receiving parent is listed first.

A. Interspecific Crosses

1. A. integrifolium subsp. integrifolium ($n = 4$) X A. condimentum ($n = 3$).

The plants of A. integrifolium subsp. integrifolium were grown from seed of plants supplied by Dr. R. B. Channell (Channell 8880).

Seven somatic chromosomes were present in the root tips of the two F_1 plants obtained (Plate 6, Fig 7). In meiosis, 50 cells showed one trivalent and two bivalents. At diakinesis, this trivalent was present as a ring or a chain (Plate 6, Fig 1 - 5). Sometimes a single univalent and a loosely associated bivalent were found, but such configurations were extremely rare. One trivalent and four univalents were observed in only two cells. Pollen stainability was a mere 2.9 per cent. This cross provided the most conclusive evidence for aneuploid reduction in Astranthium.

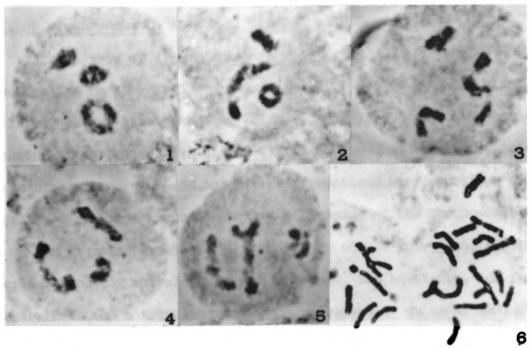
2. A. orthopodum (n = 3) X A. condimentum (n = 3).

In 80 cells examined, only a few showed two univalents at diakinesis, the remaining cells did not show any meiotic irregularities. Although normal pollen tetrads were formed, pollen stainability was only 54.0 per cent. In view of the regular meiosis observed, this relatively low percentage is noteworthy. Kruckeberg (1961) recently made similar observations on artificial hybrids between closely related species of Silene. He suggested that the reduced fertility of homoploid hybrids was due to "...genic ...or minute segmental differences, below the threshold of detection, in the chromosomes". The evidence suggests that this may also be the case in this particular instance.

3. A. purpurascens (n = 8) X A. condimentum (n = 3).

The plants of A. purpurascens used in this cross were from collection De Jong 11444. The root tip chromosomes of the three F_1 plants obtained were 11 in number (Plate 6, Fig 8). As expected, meiosis was extremely irregular, with a single trivalent, one bivalent,

Plate 6. Fig. 1 - 9. Chromosome configurations in experimental hybrids of Astranthium. Fig. 1 - 5. Diakinesis in hybrids of A. integrifolium subsp. integrifolium (n = 4) X A. condimentum (n = 3). Fig. 1. Two bivalents and a circular trivalent. Fig. 2 - 4. Two bivalents and a trivalent-chain. Fig. 5. Two bivalents, one loosely associated, and a trivalent-chain. Fig. 6. Somatic chromosomes of the hybrid A. Beamanii (n = 12) X A. splendens (n = 9), showing 21 chromosomes. Fig. 7. Somatic chromosomes of the hybrid A. integrifolium subsp. integrifolium (n = 4) X A. condimentum (n = 3), showing seven chromosomes. Fig. 8. Somatic chromosomes of the hybrid A. purpurascens (n = 8) X A. condimentum (n = 3), showing 11 chromosomes. Fig. 9. Somatic chromosomes of the hybrid A. orthopodum (n = 3) X A. purpurascens (n = 8), showing 11 chromosomes.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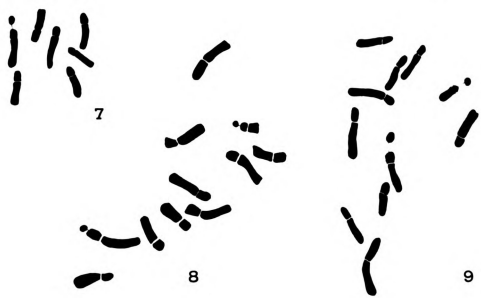

7
8
9

and six univalents observed in most instances. In other cells I found one trivalent, two bivalents, and four univalents, or three bivalents and five univalents. No stained pollen grains were found.

4. A. orthopodum (n = 3) X A. purpurascens (n = 8).

The plants of A. purpurascens used in this cross were from collection De Jong 1131. The somatic cells of the three F_1 plants clearly showed 11 chromosomes (Plate 6, Fig 9). As expected in offspring from parents with widely different chromosome numbers, meiosis was highly irregular and meiotic configurations were sometimes difficult to interpret because of extreme clumping of the chromosomes.

In 25 cells examined, 18 contained a single trivalent, one bivalent, and six univalents, or a trivalent, two bivalents, and four univalents, or a trivalent and eight univalents. In other cells, the following configurations were observed: four univalents, one bivalent, and a clump of five chromosomes; two bivalents and seven univalents; a clump of five chromosomes and six univalents; one bivalent and nine univalents; rarely, 11 univalents. No stained pollen grains were observed in the hybrids. The reciprocal cross was successful, but the single F_1 plant did not reach maturity.

5. A. splendens (n = 9) X A. purpurascens (n = 8).

Plants of A. purpurascens were from collection De Jong 1131. The following meiotic configurations were observed: one trivalent and seven bivalents; one trivalent, six bivalents, and two univalents; one trivalent, five bivalents, and four univalents; six bivalents and five univalents. In these meiotic figures, one trivalent and seven bivalents were most frequently seen. Pollen stainability was 65.0 per cent.

6. A. Beamanii (n = 12) X A. splendens (n = 9).

Five F_1 plants were obtained in this cross. The root tip chromosomes are shown on Plate 6, Fig 6. Attempts to analyze microsporogenesis failed because of the extreme clumping of the chromosomes, and observations are therefore limited. In addition to the chromosome clump, from one to five univalents were seen. Lagging chromosomes could be seen in first and second anaphase, and micronuclei formation in the tetrads was frequent. Pollen stainability was 58.5 per cent.

7. A. splendens (n = 9) X A. orthopodum (n = 3).

The two F_1 plants obtained in this cross showed 12 somatic chromosomes. The hybrids are approximately one year old and are still in the vegetative stage, consequently, it has not yet been possible to analyze meiosis.

B. Intraspecific Crosses

Early in this study, an attempt was made to ascertain whether the three widely separated populations of Astranthium purpurascens are specifically distinct.

The following intraspecific crosses were carried out:

female parent by collection	male parent by collection	hybrid pollen stainability %
De Jong 1227 (Hidalgo)	X De Jong 1131 (Oaxaca)	1.5
De Jong 1131 (Oaxaca)	X De Jong 1144 (Chiapas)	8.2
De Jong 1144 (Chiapas)	X De Jong 1131 (Oaxaca)	1.3
De Jong 1227 (Hidalgo)	X De Jong 1144 (Chiapas)	3.1

The three populations of A. purpurascens are represented by collection numbers De Jong 1227, 1131, and 1144 respectively. No differences could be observed in chromosome number and karyotypes in these collections. Taxonomic studies have indicated that there is an overlap of morphological characters, consequently, A. purpurascens is here treated as a single, if somewhat polymorphic species.

A study of microsporogenesis of each "hybrid" rarely showed any irregularities. The extremely low percentages of pollen stainability are therefore surprising. Although the three populations have not yet achieved morphological distinctness, genetic barriers appear to be present, in part possibly as a result of geographical isolation. The regular meiosis in the hybrids and the similarity in the karyotypes of the three populations would suggest that small, genic or segmental differences in the chromosomes are responsible for this reduced hybrid fertility.

FLORAL ANATOMY

The anatomical studies reported here involve both the study of whole-mount material for the purpose of comparing floral and achenial modes of vasculation, and observations on the histology of the capitula of *Astranthium* and species of other genera in the Astereae.

A. Vasculation

1. *Ray Florets*. The ray corollas of *Astranthium* are ligulate and consist of a short, sparsely pubescent tube and a flattened, expanded lamina with the apex commonly 3-toothed. The venation of the lamina typically shows four vascular bundles which originate from the vascular plexus below the apex of the ray achene. These bundles traverse the length of the lamina and converge at the apex. The corollas of some ray florets may show five, or less commonly six or even seven veins, but the four-bundled condition is by far the commonest in the genus. This type of corolla vasculation is the "Aster-type" of Koch (1930).

At the base of each ray achene, a single vascular bundle enters from the receptacle. Upon entering, this bundle divides to form two lateral bundles which traverse the length of the achene. A single ovule trace may sometimes be seen branching off the basal knot of vascular tissue, but this trace extends upward for only a short distance. The lateral achenial bundles may consist of a single row of tracheary elements or may contain several, mostly somewhat thinner, files which commonly increase in number and consequently in thickness

Table 3. Species of Astereae with two-bundled ray achenes and four-bundled ray corollas.

species	source of material (MSC)
Achaetogeron Forreri	De Jong & Longpre 1003
A. griseus	De Jong & Longpre 978
Bellis perennis	Nelson 2967
B. sylvestris	Botanical Garden, Coimbra, Portugal (MSC 166628)
Brachycome trachycarpa	Jones 126
Chaetopappa modesta	Pringle 8235
Dichaetophora campestris	Pringle 8303
Townsendia mexicana	Beaman 1887
T. Parryi	Beaman 4459
T. strigosa	Payson & Armstrong 3205

toward the apical plexus. In cross-section, the two nerves of each achene may be seen as small areas of sclerified cells, each directly opposite and external to a bundle. At the plexus, the two bundles branch, each forming two corolla bundles and one stylar bundle. Although the achenial bundles appear to be free from one another at the plexus, they are occasionally interconnected. A third, thinner bundle with a single file of tracheary elements has been observed in some ray achenes of A. orthopodum, and this bundle branches independently into a corolla bundle and a stylar bundle.

Two vascular bundles are found in the ray achenes of all species of Astranthium except A. xylopodum and A. laetificum. Whereas all other species have two-nerved achenes, the achenes of A. xylopodum and A. laetificum are prominently ribbed and the mode of vasculation in these species seems to be correlated with the position of the ribs.

The ray achenes of A. xylopodum are two- or three-ribbed, and have achenial faces which may be provided with one or two conspicuous longitudinal nerves. In cross-section, these ribs and nerves appear as areas of heavily sclerified cells. Four vascular bundles, two lateral and two dorsi-ventral, branch off a single trace which enters the base of the achene from the receptacle. In two-ribbed achenes which have a single nerve on each face, each lateral bundle is directly opposite a rib and each dorsi-ventral bundle is directly opposite a nerve. When the ray achenes are three-ribbed, one lateral bundle is opposite one rib, while the other is about midway and alternate with the two remaining ribs. The dorsi-ventral bundles are again opposite a nerve, if present.

In A. laetificum, the ray achenes are two- or three-ribbed. Two-

Plate 7. Fig. 1 - 6. Details of the vasculation of the achenes of *Astranthium*, viewed laterally. Corolla bundles, *c*; style bundles, *s*; anther bundles unlabeled. Fig. 1. Ray achene of *A. orthopodum*, X 80 (*De Jong* 984). Fig. 2. Disk achene of *A. xylopodum*, X 80 (*De Jong* 1028). Fig. 3. Disk achene of *A. laetificum*, X 40 (*De Jong* 1104). Fig. 4. Disk achene of *A. xanthocomoides*, X 80 (De Jong 1195). Fig. 5. Disk achene of *A. orthopodum*, X 80 (*De Jong* 984). Fig. 6. Disk achene of *A. purpurascens*, X 80 (*De Jong* 1144).

ribbed achenes have two vascular bundles, each bundle directly situated opposite a rib. Three-ribbed achenes have three vascular bundles, each bundle again opposite a rib. Unlike the achenes of A. xylopodum, the ray achenes of A. laetificum have nerveless faces.

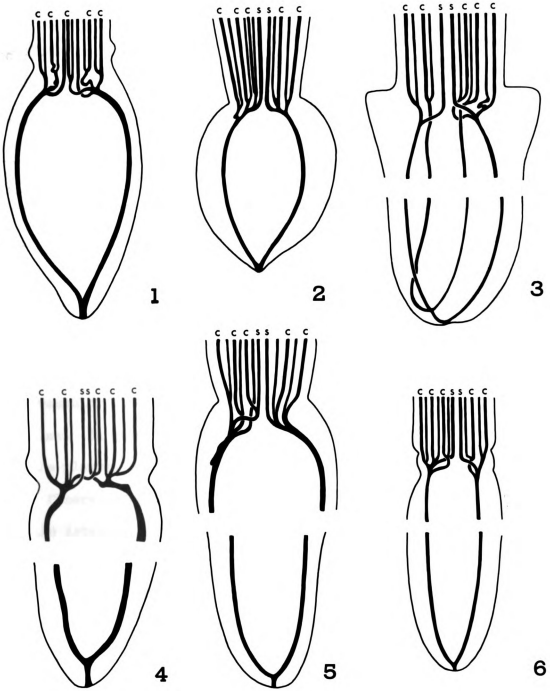
The mode of vasculation of the ray florets was investigated in detail only in Astranthium, but limited observations were also made of cross-sections of heads of species of other genera in the Astereae.

The "Aster-type" of corolla vasculation (Koch, 1930) was also observed in the species which are listed in Table 3. The ray achenes of these species also appeared to have two vascular bundles.

2. Disk Florets. The venation of the disk florets of Astranthium is that of the "typical Composite flower" (cf. Carlquist, 1961) and is the "Aster-type" of Koch (1930). The vascular supply of the corolla consists of five fused lateral bundles which extend upward through the limb and divide at the sinuses of the corolla lobes. After dividing, they run along the margins of the lobes and converge at the apices. The five stamen bundles branch off the corolla bundles in the region of the vascular plexus below the apex of the achene. On the whole, the stamen bundles are somewhat thinner than the corolla bundles, but, like the latter, they consist of a single file of tracheary elements. The style contains two vascular bundles which diverge at the bifurcation of the style branches, each bundle supplying a stylar branch and terminating just below the apex of the stylar appendages.

As in the ray achenes, a single bundle enters the achene from the receptacle. This bundle often consists of a number of rows of

Plate 8. Fig. 1 - 6. Details of the vasculation of disk achenes of species of Astereae, viewed laterally. Corolla bundles, c; style bundles, s; anther bundles unlabeled. Fig. 1. Brachycome trachycarpa, X 80 (Jones 126). Fig. 2. Dichaetophora campestris, X 80 (Pringle 2803). Fig. 3. Aphanostephus ramosissimus, X 80 (De Jong & Longpre 916). Fig. 4. Townsendia mexicana, X 80 (Beaman 1857). Fig. 5. T. formosa, X 40 (Beaman 994). Fig. 6. T. strigosa, X 40 (Payson & Armstrong 3205).


C C C C C
1
C C C S S C C
2
C C S S C C C
3
C C SS C C C
4
C C C S S C C
5
C C C S S C C
6

tracheary elements. In A. xylopodum, the bundle divides to give rise to four bundles, two lateral, and two dorsi-ventral (Plate 7, Fig. 2). These may or may not divide in turn midway between base and apex. Corolla bundles and stylar bundles branch off the apical plexus.

In all other taxa of Astranthium, the disk achenes are two-bundled. The single bundle entering from the receptacle branches to form two lateral bundles which traverse the length of the achene. As in the ray achenes, the two nerves may be seen as small areas of sclerified cells, each directly opposite and external to a bundle. Exceptions to the two-bundled condition were noted in some disk achenes of A. orthopodum in which two or three additional bundles were observed (Plate 7, Fig. 5) and in A. purpurascens, in which several achenes had three bundles (Plate 7, Fig. 6). The extra bundles either join the vascular plexus or branch independently into corolla and anther bundles. In general, the achenial bundles remain free from one another at the plexus, but they are occasionally interconnected.

Observations on cleared disk florets of species in other genera of the Asteraeae were also made. These species are listed in Table 4. As in Astranthium, the majority of species were also found to have two achenial bundles, but there were several notable exceptions.

It is interesting to note that the species of Erigeron listed in the Table which have more than two vascular bundles, also have many-nerved achenes. For example, E. canus, which Cronquist (1947) indicated as having 8 - 14-nerved achenes, was found to have 12 vascular bundles in several disk achenes. Similarly, E. argentatus has 6-, 7-, or 8-nerved achenes, and I observed 6 bundles in the few disk achenes studied. On the other hand, E. vernus, which Cronquist

Table 4. Number of vascular bundles in disk achenes of species of Asteroae.

species	number of vascular bundles	source of material (MSC)
Achaetogeron Forreri	2	De Jong & Longpre 1003
A. griseus	2	De Jong & Longpre 978
A. guatemalensis	2	De Jong 668
A. mexicanus	2	De Jong 647
A. polycephalus	2	Palmer 52 (MO)
Aphanostephus ramosissimus	4	De Jong & Longpre 916
Bellis perennis	2	Nelson 2967
B. sylvestris	2	Botanical Garden, Coimbra Portugal (MSC 166628)
Boltonia asteroides	2	McDonald 5602
Brachycome trachycarpa	2	Jones 126
Chaetopappa asteroides	2	Pringle 8235
Dichaetophora campestris	2	Pringle 2803
Erigeron argentatus	6	Jones 1823
E. canus	12	Heller 3791
E. parishii	4	Parish 2393
E. vernus	2	Tracy 9002
Townsendia formosa	2	Beaman 994
T. mexicana	2	Beaman 1857
T. Parryi	2	Beaman 4559
T. strigosa	2	Payson & Armstrong 3205

considered to have 4-nerved achenes, was found to have two achenial bundles. Although the evidence is not conclusive, it is possible that the number of achenial bundles is correlated with the number of nerves in some species. It could not be ascertained, however, whether the achenial bundles themselves or small ribs of sclerified cells constituted the actual nerves of these achenes.

Another exception was Aphanostephus ramosissimus in which the disk achenes were found to be 4-nerved. Since not all bundles are of equal thickness, it is possible that the achenes of Aphanostephus are commonly two-bundled, but that additional bundles are occasionally found. This has been observed to be the case of several species of Astranthium, as indicated above, and it has also been observed in Boltonia asteroides, in which several disk achenes were three-bundled.

B. Histology

1. Ray Corolla. As seen in trans-section, the ground tissue of the lamina of the ray florets of Astranthium consists of loosely arranged parenchyma cells. The vascular bundles are evenly spaced in this ground tissue and lie close to the abaxial epidermis. The thickness of the lamina is uniform throughout.

The most conspicuous feature of the anatomy of the ray lamina is the adaxial epidermis which consists of a single layer of large cells the outer wall of which is strongly convex and supplied with a thick, smooth cuticle. The abaxial epidermis, however, is made up of a layer of smaller cells with end walls which are rounded. The thick cuticle is sculptured into prominent, parallel, sharp-edged ridges and, therefore, appears spinose in cross-section. The strongly convex cells of

the adaxial epidermis are found throughout the lamina. In the region of the tube, however, the end walls loose their convexity and the cells decrease in size so that the cells of both epidermal layers are alike in appearance.

The ray florets of other species of Astereae examined showed no differences in the type of tissues and the position of the vascular bundles when compared with Astranthium and with one another. All have the convex adaxial epidermal cells and the sculpturing of the cuticle of the abaxial epidermis is also similar. With respect to the thickness of the vascular bundles, the lamina of Townsendia strigosa, T. Parryi, and T. mexicana have vascular bundles which are considerably thicker than those of any of the other species examined.

2. Disk Corolla. The five lobes of the disk florets of Astranthium, as in the majority of Compositae, have thickened apices. In trans-section, these apices are made up of large, rounded cells. Midway between the apices and the sinuses, the corolla lobes are four to six cells thick, including the epidermal cells. From the sinuses down to the region of the filaments, the corolla wall is only two cells thick, but more cell layers are present around the vascular bundles. In the region of the filaments, the corolla is still two cells thick, but the cells are much larger. Below the level where the filaments diverge from the corolla tube, the wall is between six and ten cells in thickness.

The presence of canals associated with the corolla veins is commonly observed. Although sometimes lacking, one, or more commonly two, canals may be seen lateral to the veins. In A. xanthocomoides,

only a single canal, which is external to the vein, may be present. In all species, these canals appear to run only for short distances, as observed in longitudinal sections of disk florets of A. integrifolium subsp. ciliatum. This condition, plus the absence of stained cell deposits, the absence of epithelial cells, and the somewhat irregular shape of the openings, suggest that these canals are air lacunae rather than secretory canals. This also holds true for the other Astereae examined, except for Aphanostephus ramosissimus. The disk florets of that species have a single canal located externally to the veins. The presence of epithelial cells indicates that these may be secretory canals. In view of other similarities of Aphanostephus to aromatic Anthemideae, the presence of secretory canals would not be surprising.

3. Phyllaries. The phyllaries of Astranthium are scarious-margined and are flattened throughout except near the base where a slight keel is present. The ground tissue of the green midportion consists of spongy mesophyll which is commonly sclerified. Palisade mesophyll and secretory canals are absent. Just below the apex where veins are absent, a single pole of sclerenchyma may be located in the center. The ground tissue becomes increasingly sclerified toward the base and the zone is interrupted by vascular bundles. Near the base, where only the midrib is present, the zone of sclerenchyma extends as a continuous band, from one to five cells in thickness, from near the midrib to as far as the innermost cells of the scarious margins. The latter are mostly two cells thick, with a single file of one to several cells constituting the very edge. The abaxial epidermis is provided

with stomata and trichomes which are lacking on the adaxial surface.

The phyllaries of Aphanostephus ramosissimus, Brachycome trachycarpa, Dichaetophora campestris, and Townsendia Parryi are similar to those of Astranthium in internal morphology. However, the phyllaries of Bellis perennis, Achaetogeron griseus, Townsendia mexicana, and T. strigosa are strikingly different.

Bellis perennis has phyllaries in two series which are herbaceous throughout, flattened, and of uniform thickness for the greater portion of their width. The ground tissue is made up of spongy mesophyll which is never sclerified. Palisade cells and secretory canals are lacking. The phyllaries of Achaetogeron griseus are in three to four series and are heavily sclerified. The outer phyllaries are relatively thick, with scattered areas of sclerenchyma, whereas the inner phyllaries are thinner and narrower and are made up of a heavy zone of sclerenchyma bounded by the two epidermal layers. In the region external to the midrib, some spongy mesophyll is present.

The organization of the phyllaries of Townsendia mexicana and T. strigosa is more complex. The phyllaries are not flattened, but are strongly keeled, the thickened midportion tapering abruptly toward the margins as seen in cross-section. The keeled portion is of considerable interest in that palisade mesophyll is present on the abaxial side, spongy mesophyll being present adaxially. At a level corresponding to that of the anthers, a continuous zone of sclerenchyma extends from the outer cells of the keeled portion to as far as the prominent scarious margins which are one to two cells thick. In the narrowed portion of the phyllaries, away from the midrib, sclerified tissue is bordered only by the two epidermal layers. In T. strigosa,

at a level corresponding to that of the achenes, palisade mesophyll is lacking and a continuous band of sclerenchyma traverses the entire width of the phyllaries, as far as the scarious margins. In *T. mexicana*, at a corresponding level, this band of sclerenchyma is interrupted in the region of the midrib.

MORPHOLOGY

HABIT. The habit of the species of Astranthium is closely correlated with their life history. At the beginning of the flowering season the plants are small and commonly have a single, monocephalous stem. All but one species in the genus possess a basal rosette at that time. The exception is A. xylopodum, which, on the basis of observations on herbarium material and greenhouse-grown seedlings, appears to lack a basal rosette.

As the season progresses, other stems develop, branching occurs, and the plants gain in height. The capitula that are still in bud are typically cernuous, the peduncles elongating and straightening just prior to anthesis. In most species the basal leaves and lower cauline leaves wither, but they are mostly persistent in A. splendens and A. Beamanii. Near the end of the growing season secondary flowering often occurs in the annual species, resulting in the formation of numerous, smaller heads with fewer ray and disk florets. At the end of the season the plants set seed and the annual species die. The perennial species form a new basal rosette and the stems die back and often persist as dried stalks well into the next flowering season.

Three species of Astranthium are annual, one is biennial or short-lived perennial, and six species are perennial. Greenhouse cultures have indicated that the perennial species are capable of coming into flower as quickly as the annual species.

The interpretation of A. xanthocomoides as a perennial species

requires an explanation. In greenhouse cultures, plants of A. xanthocomoides grew vegetatively during the first half of the summer of 1962 after seeds germinated early that spring. During this time, single parent plants would give rise to numerous stolons which established new plantlets at their tips. In the beginning of September the parent plants formed a single flowering stem after the plants had lost their basal rosette. Following flowering, the parent plants died about the middle of October and those portions of the stolons closest to the parent plants also died. Even though the species showed a pattern of growth typical of other annual species in the genus, it is clearly perennial through stolons.

STEMS. The stems of the annual species of Astranthium are usually numerous and much-branched above as well as below the middle. The stems of the perennial species are branched to a lesser degree and in a more open fashion than the annual species. In most species, the stems are spreading, ascending, or erect, but the stems of the annual A. condimentum and A. robustum are often strongly decumbent. The perennial A. laetificum approaches being scapose while the perennial A. xanthocomoides has few to numerous stolons in addition to the flowering stems. Stem structure may therefore provide useful characters for separating species or species groups. Stem color is uniform throughout the genus, varying from greenish through greenish-brown to reddish-purple. The stems of all species are grooved and striate, the ribs being of a lighter color than the grooves.

Peduncles are conspicuous in all species of Astranthium and are naked except for the occasional presence of one, rarely two, minute, linear bractlets. Where they join the capitulum, the peduncles are

enlarged, often hollow, and sparsely to densely strigose. Before anthesis, the peduncles are inconspicuous, the closed heads terminating leafy stems.

ROOTS. All but one of the perennial species of Astranthium have a fibrous-rooted, branched or unbranched caudex that may be vertical, oblique, or horizontal. The exception, A. xylopodum, has a stout, woody taproot which develops a thick bark. The roots are useful in separating the annual species which are characterized by fibrous roots or slender, light-colored taproots with or without fibrous secondary roots. The taproot of the biennial or short-lived perennial A. orthopodum possesses a swollen stem-root junction that may be solid or hollow.

LEAVES. The leaves of Astranthium are alternate and are very similar in shape, texture, and pubescence. The basal leaves are the largest and widest in each species and the width is correlated with the width of the cauline leaves. Thus a narrow-leaved species such as A. orthopodum has correspondingly narrow basal leaves. Since the basal leaves and lower cauline leaves taper gradually toward the leaf-stem junction, there is no differentiation between lamina and petiole. The middle and upper cauline leaves are sessile. The leaf margins of all species are entire, with the exception of A. laetificum which sometimes has a few leaves which may have from one to five minute teeth above the middle. Leaf gradation, from spathulate or oblanceolate basal leaves with blunt or mucronate apices to small, linear-lanceolate upper leaves with acuminate apices is striking in the genus. In A. xylopodum and A. laetificum, leaf gradation is less strongly expressed. Leaf venation has been found distinctive in A. xylopodum as the leaves

of that species are consistently three-nerved in contrast to the one-nerved leaves of the other species.

PUBESCENCE. The stems and leaves of Astranthium are characterized by a strigose pubescence. The trichomes are three- to eight-celled and have an enlarged basal cell and an elongated terminal cell constituting the sharp-pointed apex. The trichomes of the leaves are always somewhat appressed, especially in herbarium specimens, whereas those of the stems are appressed or spreading. The coarsest trichomes are found in the Hinton, Palmer, and Pringle collections of A. xylopodum; here they may reach 2.0 mm in length.

INVOLUCRE AND RECEPTACLE. The phyllaries of Astranthium are flattened and usually imbricated in two series. The margins are scarious and ciliate or lacerate-ciliate mostly above the middle. The green midportions of the phyllaries are glabrous to densely strigose on the outside and shiny and glabrous within. Phyllary shape ranges from broadly ovate to linear-lanceolate and the apices vary from acute to ciliate-acuminate, often within the same species. Phyllary length is occasionally a useful character, but most species cannot be differentiated on the basis of phyllary length alone.

The receptacle of Astranthium is conical. It is low-conical in A. xylopodum but in all other species tends to become steeply conical at maturity. Since Astranthium lacks a pappus for seed dispersal, it is possible that a steep, conical receptacle promotes short-distance wind dispersal by elevating and exposing the mature achenes above the level of the phyllaries.

The surface of the receptacle is alveolate in all species, with a ring of small setae surrounding the achenial attachment points. In

mature plants, the receptacle is hollow, the cavity being an upward extension of that of the swollen apex of the peduncle.

FLOWERS. The ray florets are pistillate and fertile and occur in a single series. Ray color has proven to be a useful taxonomic character when used in conjunction with other characters. The majority of species of Astranthium has white rays, but four species have cyanic rays that are light lavender above and dark lavender below. One species, A. Beamanii, has rays which are lavender throughout or which are lavender above and with alternating bands of light and dark lavender below. These rays nearly always become blue when dried.

The length and width of the ray corolla is too uniform to be of much value in classification. The tube of the ray is always pubescent with short, blunt trichomes and the apex is usually three-toothed. The style branches are typical of those of other Astereae; one style branch is sometimes considerably shorter than the other but this character is not constant in a species.

The disk florets are yellow, five-lobed, and "goblet-shaped", being abruptly contracted in the throat. The limbs of the disk florets of A. xylopodum are somewhat less contracted below. The length of the disk florets is only useful in distinguishing A. xylopodum from the remaining species of the genus, although there is some overlap.

Anther characters are too intangible to be of much value. An apical appendage is always present and the anther bases are rounded. An interesting feature which commands attention concerns the color of the erectile tissue of the filaments as observed in greenhouse cultures. With the exceptions of two collections of A. purpurascens (De Jong 1131 and 1227), the erectile tissue contains a bright orange pigment before

anthesis. This feature may be observed in dried specimens. After anthesis takes place, the erectile zone elongates and the color changes from bright orange to pale yellow.

Pollen characters are of little value in the delimitation of the majority of species of Astereae (Wodehouse, 1959) and this has also been found to be the case in Astranthium. Measurements of the diameter of the grain, spine length, and exine width were observed to overlap to such an extent that separation of the species on the basis of these features was not possible. As in other Astereae, the pollen of Astranthium is spheroidal, tricolpate, and uniformly spinose.

ACHENES AND PAPPUS. Achenial characters have been very useful in separating groups of species. In Astranthium, achene shape varies from obovate to oblanceolate and the achenes are laterally compressed. The achenes of A. xylopodum and A. laetificum are set apart from those of the other members in the genus by their large size, lack of pubescence, and the presence of prominent ribs. A. xylopodum has achenes which are two- to four-ribbed and the ribs are lighter in color than the achenial faces which may have up to two conspicuous, longitudinal nerves. The achenes of A. laetificum are two- or three-ribbed but the ribs are less conspicuous than the achenial ribs of A. xylopodum. The three-ribbed achenes are triquetrous in both species.

The remaining members of the genus have small to medium-sized achenes which are prominently or obscurely two-nerved, lacking true ribs. Sometimes these achenes are slightly triquetrous due to pressure exerted by neighboring achenes on the receptacle. Pubescent achenes typically have achenial hairs which are duplex, with two connate cells which are recurved distally. This type of glochidiate pubescence is

also found in Dichaetophora and Townsendia and underscores the relationships of these two genera with Astranthium.

The pappus of Astranthium is on the whole inconspicuous and may be present or lacking in the same species or even in the same capitulum. Except in A. xylopodum where it is lacking, the pappus consists of a minute, yellowish, whitish, or sometimes brownish ring or crown of setae less than 0.1 mm long. The pappus is most conspicuous in A. laetificum and A. orthopodum but this may vary even within the same head. Pappus characters are therefore of no value in distinguishing taxa.

DISTRIBUTION AND ECOLOGY

Astranthium is primarily a Mexican genus with eight of the ten species in the genus represented in the montane regions of that country. Two species are found in the United States, one of which, A. integrifolium, ranges southward into the state of Nuevo Leon in northeastern Mexico. The distribution pattern of the Mexican species is typically Y-shaped, extending along the Sierra Madre Occidental, the Sierra Madre Oriental, across the Trans-Volcanic Belt of South-Central Mexico and southward into the mountains of Oaxaca and Chiapas. No species of Astranthium are known from Central America.

The majority of the Mexican species of Astranthium occurs between 1700 and 2900 meters elevation, but A. xylopodum is found between 800 and 1500 meters in western Mexico. In addition, A. Besmanii occurs at altitudes from 2700 to 3700 meters on Cerro Potosi in Nuevo Leon where it reaches alpine elevations.

Three species are found in western Mexico. The northernmost of these, A. orthopodum, occurs in the Sierra Madre Occidental in Chihuahua and Durango, reaching its southern limit in central Durango. Another western species, A. condimentum, ranges from east-central Michoacan westward and then northward into Jalisco. The range of A. xylopodum partly overlaps that of A. condimentum, but the two species are separated from each other altitudinally. In eastern Michoacan, only two localities are known for A. laetificum; one of these is at ca. 2500 meters elevation in the Transvolcanic Belt.

Among the eastern species, A. purpurascens is the most widely

distributed. Its range is made up of three populations that are separated by considerable geographic gaps. The northernmost of these populations is in the Sierra Madre Oriental in San Luis Potosi and Hidalgo while the other two are in the mountains of Oaxaca and Chiapas respectively. Another eastern species, A. xanthocomoides, occurs in the Sierra Madre Oriental in Hidalgo and in the easternmost mountains of the Transvolcanic Belt in Puebla, Tlaxcala, and Veracruz. Although both A. purpurascens and A. xanthocomoides are found in Hidalgo, their ranges do not overlap. The remaining eastern species occur in Nuevo Leon where A. Beamanii is endemic to Cerro Potosi, principally at alpine and subalpine elevations. Another endemic, A. splendens, ranges from south of Cerro Potosi southward into Cerro Linadero and east into adjacent Tamaulipas.

Most of the Mexican species of Astranthium are narrow endemics. Three are confined to one state, two species are found in two states, one species occurs in three states, and two are found in four states. All eight of these species occur in montane habitats, but each is separated from neighboring species by geographical or ecological barriers. It is probable that present distribution patterns reflect past changes in both physiography and climate.

All species except A. xylopodum occupy cool, relatively moist open meadows and open pine-, pine-fir-, and pine-oak forests mostly on brown sandy loams and reddish clay loams. The habitat of A. xylopodum is considerably drier than that of the other species, ranging from arid oak forests at 800 meters elevation to semi-arid pine-oak forests at about 1500 meters. Of the Mexican species, A. purpurascens occupies the most diverse habitats apparently as a consequence of its

wide distribution. In addition to open meadows and pine forests, this species is also found in open Quercus-Taxodium stands and open Pinus-Quercus-Juniperus associations. All Mexican species of Astranthium are members of the temperate vegetation zone and belong to the boreal forest- (annual rainfall 30 - 74 inches) and pine-oak forest (annual rainfall 18 - 70 inches) communities (cf. Leopold, 1950).

The United States species Astranthium integrifolium is the geographically most widespread member of the genus; it is here recognized as comprising two subspecies. Subspecies ciliatum ranges from Nuevo Leon, Mexico, where it reaches elevations of 2500 ft. through east-central Texas northward into Oklahoma and the southernmost counties of Kansas and Missouri and eastward into Arkansas where it overlaps with subsp. integrifolium. In Texas, subsp. ciliatum occupies six different vegetational areas at elevations ranging from sea level to about 800 ft. (Gould, 1962). Although differing in species composition, these vegetational areas are predominantly characterized by acid sandy or sandy loam soils. On the basis of distributional data obtained from herbarium labels, subsp. ciliatum has its greatest concentration in the Gulf Prairies and Marshes, Post Oak Savannah, and Blackland Prairies vegetational areas, with average annual rainfall ranging from 30 to 50 inches.

In Oklahoma, A. integrifolium subsp. ciliatum is confined to the eastern half of the state. On the basis of distribution data, subsp. ciliatum occupies four major vegetation zones as outlined by Bruner (1931), the true prairie and oak-hickory savannah associations in central and east-central Oklahoma, and the eastern grassland and oak-hickory forest associations in the eastern part of the state.

Corresponding average annual precipitation increases eastward, ranging from 30 inches in the central portion of the state to 45 inches in the east.

The eastern part of the range of A. integrifolium is occupied by subsp. integrifolium. This subspecies ranges from Arkansas, where it overlaps with subsp. ciliatum, eastward to Tennessee and Kentucky and southward into central Mississippi and the northern parts of Alabama and Georgia. Available collection data from herbarium specimens indicate that this subspecies occupies calcareous soils in relatively dry to moist, open to shady woodland habitats.

The last species under consideration is A. robustum which is a narrow endemic found only in the Trans-Pecos region north of Big Bend National Park in extreme western Texas at elevations between 2900 and 4800 ft. A. robustum occupies habitats ranging from arid pinehill flats and open, arid roadsides to arid canyons in the mountains on soils that are predominantly alkaline. Ecologically, A. robustum is a member of the "Trans Pecos, Mountains and Basins" vegetational area of Gould (1962), which is characterized by an average annual rainfall of less than 12 inches. Although the region in which A. robustum is found borders on Chihuahua, the species has not been reported from Mexico; it is also unknown from Big Bend National Park.

EVOLUTION

A. Origin.

Since Astranthium is primarily a Mexican, montane genus restricted to the Sierra Madre Occidental, the Sierra Madre Oriental, the Transvolcanic Belt, and the mountains of central Oaxaca and central Chiapas, it is thought that the evolution of the genus is closely correlated with the physiographic history of these mountain ranges.

Schuchert (1928) suggested that the present relief of Mexico was the result of elevation and block faulting in the late Pliocene and Pleistocene. Thayer (1916) indicated that the Transvolcanic Belt owed its relief to vulcanism starting in the Pliocene. White (1962) considered the oldest volcanic rocks exposed along the lowermost western slopes of Iztaccihuatl to be of mid-Tertiary age. According to Garfias and Chapin (1949), the Sierra Madre Occidental was uplifted in the Miocene, the Sierra Madre Oriental in the Pliocene, and the Sierra de Chiapas in late Pliocene. The present high relief of much of Mexico is thus considered to be of relatively recent origin.

During the Tertiary, concomitant with orogenic events, there was a gradual, worldwide trend toward cooling and drying (Axelrod, 1960), culminating in the great ice advances of the Pleistocene. Dillon (1956) postulated that during the Pleistocene, "...there appears to have occurred at that period of maximum glaciation a clinal depression of meantemperatures that amounted to 5° F at the equator, to 10° F at latitudes 35° to 40° N, and to 25° at the edge of the ice

sheet". Decreases in water temperatures as well as in the level of the oceans were also evident at that time (Emiliani, 1955; Flint, 1957). Climatic cooling during the Pleistocene may be inferred from the presence of glacial features on Iztaccihuatl at elevations as low as 2450 m (White, 1962), indicating an altitudinal difference of about 2000 meters between existing and former glaciers. Additional evidence was presented by Lorenzo (1959) who noted the presence of glacial features on mountains which do not have glaciers at the present time. Sears and Clisby (1952), in a study of soil-cores from Mexico City, showed a correlation between continental glaciation and the composition of fossil-pollen profiles, as indicated by the presence or absence of pollen of upland species of trees at different depths. They concluded that "....moist and/or cool conditions represent periods of ice advance, whereas dry and/or warm represent intervals of retreat". In Central America, past cooler climates are indicated by evidence of glaciation on Cerro Chirippo in the Sierra Talamanca, (Weyl, 1955), and by pollen profiles suggesting major depressions of vegetation zones in Costa Rica (Martin, 1961). Martin (1958), summarizing environmental changes during the Pleistocene in western North America and Central America, postulated a 4000 to 4500 foot downward displacement of biotic zones in the southwest during the period of maximum glaciation. On this basis, Baker and Greer (1962) suggested that in response to Pleistocene climatic cooling, temperate plants and animals were able to migrate along the Sierra Madre Occidental which served as a chain-like avenue of dispersal. During the Pleistocene, the Sierra Madre Oriental, the Sierra Madre del Sur, and the mountains of central Oaxaca and central Chiapas must also have

served as principal migration routes for temperate biota.

Although temperate plants may have existed in Mexico since early Tertiary or even Cretaceous times (McVaugh, 1952), it has been suggested by Sharp (1953) and Dressler (1954) that the Pleistocene was the most favorable time for the dispersal of temperate plants. Similarly, Raven (1963) indicated that dispersal of the majority of temperate disjuncts in North and South America may have taken place during the late Pliocene or Pleistocene. With respect to Astranthium, Pleistocene dispersal and evolution of the genus is strongly suggested by several lines of evidence: (1) the genus is of limited distribution and nearly all species are endemics; (2) species which are related on the basis of morphological characters often occupy adjacent ranges; (3) many species have some genic material in common, as indicated by artificial crosses, suggesting recent divergence from ancestral stock. This evidence is especially impressive in the light of the fact that in rapidly evolving herbs such as Astranthium, chromosomal differences may build up rapidly.

It seems most likely that the ancestral stock of Astranthium originated in west-central Mexico where the most primitive species, A. xylopodum, is found. The range of the next most primitive species, A. laetificum, is only about 150 miles to the east. The morphological gap between the primitive species with chromosome numbers on a base of $x = 5$ (A. xylopodum and A. laetificum) is considerably greater than the gap between any pair of species in the $x = 4$ and $x = 3$ series. Astranthium xylopodum may thus be considered to be older than the other species. Furthermore, it occurs in relatively dry, low elevation habitats which have been in existence in Mexico during much of

the Tertiary. On this basis, the Pliocene seems to be a likely time during which A. xylopodum might have originated. As Tertiary orogeny and vulcanism increased the availability of temperate montane habitats, some populations of A. xylopodum may have moved into these scattered and biologically open habitats. The closely related A. laetificum may have originated directly from these populations.

When additional cool, montane habitats became available during the Pleistocene, stock of Astranthium was able to spread along montane avenues of dispersal across Mexico. This may have taken place during each of the cold periods of the Pleistocene. Increasingly warm inter- and post-glacial conditions may have been responsible for disjunction and further evolution. It is possible, that the last warming trend gave rise to the present-day species. During the last, or perhaps one of the earlier warm, dry periods, some stock of Astranthium migrated northward along the Sierra Madre Oriental into the Trans-Pecos region of Texas and became specialized as a result of adaptation to xeric conditions, forming A. robustum. Closely related stock migrated northward into the south-central and east-central United States and became differentiated into two subspecies. One of these, A. integrifolium subsp. ciliatum, appears to occupy somewhat drier habitats than does the other, subsp. integrifolium. The distribution pattern of the genus indicates that geographic isolation has played an important role in the evolution of the species. This appears also to be the case in the closely related genus Townsendia. However, where no sexual polyploids are known to exist in Townsendia (Beaman, 1957), polyploidy is an additional factor which may have played a role in the evolutionary pattern of Astranthium.

Tests for self-compatibility in Astranthium have indicated that all species are self-fertile. Self-fertility greatly facilitates migration since a single achene, landing in a favorable locality, is potentially capable of forming a new population. In Astranthium, migration was likely accomplished by relatively short-distance jumps, since the achenes lack pappus barbs or bristles for either animal or wind dispersal. It is possible, however, that some wind dispersal takes place, since the conical receptacle elevates the small achenes above the phyllaries, allowing them to be detached by gusts of wind and blown perhaps for considerable distances.

The Isthmus of Tehuantepec, which separates the Oaxaca and Chiapas populations of Astranthium purpurascens, (cf. Plate 14), may serve as an example of an area which may have been crossed by Astranthium in a single jump. The presence of tropical Miocene fossils (Berry, 1923) indicates that this area was covered with tropical vegetation during much of the Tertiary. The dispersal of these tropical species was apparently uninterrupted, since evidence for the absence of Cenozoic seaways across the Isthmus is now well documented (Durham et al., 1955). It also appears that the Isthmus has always been an area of low relief (Schuchert, 1935) and even today the highest elevation is a mere 825 ft (Baker, 1930) on the continental divide. Although Stuart (1951) suggested that during the Pleistocene, "...a relatively cool environment must certainly have formed a bridge across the relatively low Isthmus of Tehuantepec", it is doubtful whether climatic conditions were ever cool enough for temperate plants to exist in the area. For example, a downward depression of vegetation zones of 4000 to 4500 ft, as postulated for more northern areas by

Martin (1958), would be insufficient to establish a zone of temperate vegetation on the Isthmus. It seems highly probable, therefore, that the Isthmus of Tehuantepec has always been tropical, even during the time of maximum glaciation, and that temperate species such as Astranthium purpurascens crossed this tropical gap by a single jump. Analyses of pollen profiles could be of great interest in this respect, but such studies have not yet been carried out in the Isthmus of Tehuantepec.

B. Evolutionary Trends.

The interpretation of evolutionary trends in Astranthium is based on three principal kinds of indirect evidence. (1) There are morphological (and likely also physiological) specializations which may be inferred from distribution patterns and habitat requirements of the species. (2) Similar changes have taken place in several characters in both Astranthium and related genera, and these apparently are correlated. (3) There has been a general tendency for reduction in various parts of the plant body.

Primitive and advanced characters in Astranthium (cf. Table 5) inferred from the distribution and habitats involve primarily the perennial habit and the woody taproot or fibrous roots. The species which have these characters occupy relatively mesic areas within the range of the genus, whereas the annuals with slender taproots occur in drier habitats. This trend may also be inferred from the physiographic history of the areas in which Astranthium occurs (see under Origin). Similar

Table 5. Evolutionary trends in Astranthium.

primitive characters	advanced characters
1. perennial habit	annual habit
2. woody taproot	fibrous-rooted caudices to slender taproots
3. little gradation in length and width of cauline leaves	strong, upward gradation in length and width of cauline leaves
4. few, large heads	numerous, relatively small heads
5. long phyllaries	short phyllaries
6. phyllaries with narrow scarious margins	phyllaries with wide scarious margins
7. large floral parts	smaller floral parts
8. large achenes	small achenes
9. glabrous achenes	glochidiate-pubescent achenes
10. achenes with 2 or 3 conspicuous ribs	achenes 2-nerved
11. achenes with more than two vascular bundles	achenes with 2 vascular bundles
12. basic chromosome number $x = 5$	basic chromosome number $x = 3$
13. diploidy	polyploidy
14. large chromosomes	small chromosomes
15. symmetrical karyotypes	asymmetrical karyotypes

interpretations have been applied to many other groups of plants.

A considerable number of evolutionary trends in Astranthium are apparently correlated. Correlated resemblances are indicative of phylogenetic relationships (Ownbey and Aase, 1955), and by the same token related species subjected to similar environmental stresses are likely to undergo parallel evolutionary changes. The species with primitive root structure also shows little gradation in leaf size, and it has few, large heads, long phyllaries with narrow scarious margins, large floral parts, large, glabrous achenes with two or three conspicuous ribs, the highest basic chromosome number, the largest chromosomes, and the most symmetrical karyotype. In addition, the most primitive species of Astranthium has more achenial bundles than any other species and this is considered to be a primitive character (cf. Carlquist, 1961). Babcock's (1942) studies on Crepis provides additional support for the interpretation of the higher basic chromosome numbers, the larger chromosomes, and the symmetrical karyotypes as primitive characters. The most primitive species of Townsendia also has almost all of the same characters (cf. Beaman, 1957) as those which are interpreted as primitive in Astranthium. The trends of specialization in Townsendia are also similar to those in Astranthium. The species of Astranthium which seems to qualify as the most primitive species of the genus is A. xylopodum; it is characterized by all of the primitive characters listed in Table 5. It does not necessarily follow, however, that because certain characters occur in a species which is primitive, that all characters are primitive. In a genus as relatively young as Astranthium (see under Origin), however, there is a greater probability that most

primitive characters have been retained than may be true in relatively older genera.

The trends in specialization almost all involve reduction. The slender taproots of the annuals is presumably reduced from the woody taproot or fibrous roots of the perennials. Gradation in the cauline leaves is the result of reduction of the upper and middle leaves. The change from large heads to small heads, long to short phyllaries, large to small disk florets, large to small achenes, ribbed achenes with more than two vascular bundles to nerved achenes with only two vascular bundles, from $\underline{x} = 5$ to $\underline{x} = 3$, and from large to small chromosomes are all features of reduction.

Very few features of elaboration are evident in Astranthium. Polyploidy is perhaps the most obvious of these, and the change from few heads to numerous heads, and from glabrous achenes to glochidiate-pubescent achenes may involve elaboration. The latter trend is also evident in Townsendia. Evolutionary change through reduction probably has a greater probability of occurrence than change through elaboration (Stebbins, 1950). It is likely that in a recent and rapidly evolving genus such as Astranthium features of reduction would be more frequent than those of elaboration.

TAXONOMIC CONCEPTS

In Astranthium, I have recognized as species taxa which are morphologically distinct at all times and which are isolated from one another by various barriers to gene exchange. These barriers are primarily geographical and ecological. All species in the genus are allopatric and no interspecific hybrids are known. This would suggest that the present-day species of Astranthium have achieved their distinctness while being spatially isolated from each other.

When species are crossed experimentally, partial or complete sterility barriers become evident. Homoploid hybrids have reduced fertility possibly because of minute genic or structural differences in the chromosomes. On the other hand, heteroploid hybrids may be completely sterile, especially when parents with widely different chromosome numbers are crossed. These partial or complete genetic barriers are present both at the diploid and polyploid level.

Where chromosomal races differ from one another in a few, but constant characters, and, in addition, are separated by geographical and ecological barriers, I have considered these to be distinct species. The hexaploid A. splendens and the octoploid A. Beamanii may serve as examples in this respect.

I have recognized as subspecies geographic races which differ morphologically in relatively constant, mostly quantitative characters, which occupy considerable ranges, and which intergrade in the area where their ranges come into contact.

GENERIC RELATIONSHIPS

The generic relatives of *Astranthium* are not revealed by the nomenclatural history of the species in the genus. Most taxa treated by Larsen (1933) and accepted in the present monograph were transferred by her from *Bellis*, except *A. xanthocomoides* and *A. xylopodum* which were in *Brachycome* and *Koerlia* respectively.

Although *Bellis* and *Astranthium* were long considered as congeneric, the two genera have little in common. The species of *Bellis* are scapose and have few, relatively wide, herbaceous, biseriate phyllaries with blunt apices, and large, mostly glabrous, ribbed achenes. *Astranthium* species are caulescent and have numerous, scarious-margined, mostly biseriate phyllaries with acute or acuminate apices. Furthermore, the distant geographic separation argues against any close ties between the two genera since *Bellis* is primarily found in the Mediterranean region, although adventive in North America (*B. perennis*).

Arnott (in Hooker, 1835) suggested that *Bellis integrifolia* (*Astranthium integrifolium*) was the same species as *Brachycome xanthocomoides* (*Astranthium xanthocomoides*). It is perhaps for this reason that Hoffmann (1894) placed *Astranthium* in synonymy under *Brachycome*. In her monograph of the Australasian *Brachycome*, Davis (1948) concluded on the basis of a study of achenes and phyllaries that *Bellis*, *Astranthium* and *Brachycome* originated from a common ancestor, with *Astranthium* and *Brachycome* the closest of the three

genera. Although Brachycome resembles some species of Astranthium in the shape of the achenes, the most primitive, scapose, fibrous-rooted and small-headed species of that genus are very different from the caulescent, taprooted and large-headed A. xylopodum, the most primitive species of Astranthium. Furthermore, the leaves of Brachycome are commonly toothed or variously dissected whereas the leaves of Astranthium are almost always entire.

Since distant geographic separation is an additional factor that argues against any relationship of Astranthium with either Bellis or Brachycome, it seems reasonable to suggest that the generic relatives of the genus should be sought among North American or Mexican Astereae. Larsen (1933) thought the genus to be related to Keerlia, Achaetogeron, and Aphanostephus. The genus Keerlia is now in Chaetopappa (Shinners, 1946a) which is well set apart from Astranthium by the often high and narrow involucre, the unequal phyllaries in 2 - 6 series, the flat or slightly convex receptacle, and few- to many-nerved, compressed or subterete achenes. Shinners (1946b) considers Chaetopappa to be related to Leucelene. The relationships between Astranthium and Achaetogeron are not apparent following the removal of Astranthium mexicanum and A. guatemalense. On the other hand, Achaetogeron is most closely related to Erigeron and may actually belong in that genus (De Jong and Longpre, 1963).

A relationship between Astranthium and Aphanostephus is indicated by the conical receptacle, the scarious-margined phyllaries, and the basic chromosome numbers of $x = 3$, 4, and 5 which the two genera have in common. Aphanostephus is unlike Astranthium, however, in the unequal, chartaceous phyllaries in 3 - 4 series, and curved, columnar achenes as well as leaves that are toothed to deeply pinnatifid in

most species.

Shinners (1946c) included Astranthium in an arrangement of genera of Asteraeae on the basis of the conical receptacle that these genera have in common. Of these genera, Astranthium, Dichaetophora, and Boltonia fall into one group on the basis of key characters. Beaman (1957) considered Townsendia also to be a member of this group because of the conical receptacle in T. formosa. He indicated that Townsendia and Dichaetophora were the closest members of this alliance, with Astranthium somewhat more distant and Boltonia further removed. A study which I have made of the four genera suggests that Astranthium and Townsendia are even closer than previously indicated by Beaman.

A close relationship between Astranthium and Townsendia is indicated by the nature of the achenes which are obovate or oblanceolate and often glochidiate-pubescent, by the scarious-margined phyllaries and the conical receptacle. The leaves of both genera are entire, spathulate to linear and strongly reduced upward and have similar pubescence. Furthermore, Astranthium orthopodum has a swollen stem-root junction which is matched in several species of Townsendia, and lavender rays are found in species of both genera. Most important is the fact that both genera are montane and their centers of diversity are not far apart in the cordillera of the southern United States and Mexico respectively (cf. Beaman, 1957). This would suggest that the two genera have had a somewhat similar evolutionary history, although apomixis, common in Townsendia, is unknown in Astranthium. As in Townsendia, latitudinal and altitudinal influences are important in the distribution of the montane species of Astranthium and narrow endemism prevails in both genera. On the whole, Astranthium requires

more mesic conditions than Townsendia, although A. robustum parallels the more specialized species of Townsendia in its arid habitat and alkaline soil requirements. Morphologically, Townsendia appears to be less specialized than Astranthium in the relatively wide, 2 - 7-seriate phyllaries, the large number of ray florets in some species, and ribbed achenes.

Astranthium is also related to Dichaetophora (cf. Shinners, 1946c). In addition to the conical receptacle, the two genera have in common equal, scarious-margined phyllaries in two series, disk florets which have the limb abruptly contracted at the throat, and glochidiate-pubescent, compressed achenes. In habit, Dichaetophora campestris is very close to A. integrifolium, especially subsp. ciliatum. Dichaetophora differs from Astranthium, however, in the presence of a small but conspicuous squamellate pappus and prominently winged achenes which indicate a relationship with Boltonia with which the genus was formerly united by Bentham and Hooker (1883). Boltonia is clearly related to Aster and Erigeron and is distant from Astranthium.

Further references to the generic relatives of Astranthium may be found in the section on the subtribal position of the genus.

THE SUBTRIBAL POSITION OF ASTRANTHIUM:

THE DISPOSITION OF THE GENERA OF THE ASTEREAE-BELLIDINAE

Astranthium has been assigned conventionally to the subtribe Bellidinae (in synonymy under Brachycome) by Hoffmann (1894) and was considered to belong to the "Bellis-type" by Bentham (1873). The subtribe is separated from the closely related subtribe Asterinae mainly on the basis of the reduced pappus. Hoffmann considered this separation to be artificial and Shinners (1949) indicated that the subtribe Bellidinae itself "... as defined by Hoffmann... is decidedly heterogeneous and artificial".

Since Astranthium has been found in this study to be more closely related to genera in the Asterinae, a survey of herbarium material of the remaining genera of the Bellidinae was undertaken in order to assess their relationships. The results of this survey fully agree with Shinners' observations and indicate that these genera are not at all, or only distantly related to each other and that they have closer congeners elsewhere on the basis of characters other than those of the pappus.

With reference to the generic relatives of Astranthium, it has been pointed out that the genus has no close relatives in the Bellidinae but is closely related to Townsendia and Dichaetophora in the Asterinae. This close relationship certainly supports the placement of Astranthium next to these genera in the Asterinae.

Of the New World genera of the Bellidinae, Koerlia is now in

Chaetopappa (Shinners, 1946a) and Eglotes has been placed in the subtribe Grangeinae near Grangea (Shinners, 1949). I concur fully in the disposition of these two genera. The genus Greenella was considered by Solbrig (1960) to form a close alliance with Amphipappus, Amphiachyris, Guttierrezia, and Xanthocephalum in the Solidagininae and is well-placed in that subtribe, differing mainly in the color of the rays. The close relationships of the Mexican genus Achaetogeron with Erigeron were discussed by Cronquist (1947) and more recently by De Jong and Longpre (1963) and the genus is certainly to be placed next to Erigeron in the Asterinae. The genus Aphanostephus, related to Astranthium and other genera of the Asterinae having a conical receptacle, is not out of place in that subtribe if grouped with these genera.

Of the remaining genera, the European Bellis has no close relatives in the Bellidinae but is most closely related to Bellium and Bellidiastrum in the Asterinae with which it may be placed on the basis of the scapose habit, spathulate, toothed or entire radical leaves, herbaceous, biseriate phyllaries, and ribbed achenes which the three genera have in common.

The Australasian genus Brachycome often has pappus bristles which are no more reduced than those of many members of the Asterinae and in all other characters the genus is clearly a member of that subtribe. It has no close relatives in the Bellidinae, whereas it is related to Calotis and Minuria in the Asterinae (Bentham, 1873). It is suggested, therefore, that Brachycome be placed with these two genera. Dr. Gwenda Davis, who has monographed both Brachycome and Calotis, concurs fully in my disposition of Brachycome (personal communication).

The genera Rhynchospermum, Myriactis, Lagenophora, and Solenogyne are related on the basis of achenial characters, phyllaries which are mostly chartaceous and scarious-margined, and ray florets which are often greatly reduced. The achenes of the four genera are similar in shape, texture, and nervation and often have a conspicuous beak which may be produced into a sticky, glandular ring. In some species of Myriactis and Lagenophora this beak is reduced and the glandular ring is essentially sessile. Rhynchospermum and Myriactis are caulescent and have ray florets which are mostly multiseriate and much reduced, often tubular. The ray florets of Lagenophora are in 1 to few series and are also reduced although never tubular. The genus Solenogyne is considered to be derived from Lagenophora by Davis (1950), differing mainly in the tubular or very short-lipped ray florets. The combined characters of the four genera are typical of the subtribe Grangeinae and it is suggested that these genera be placed in that subtribe. This transfer also receives support from the fact that Bentham (1873) referred to Rhynchospermum and Myriactis as belonging to the "Grangea-type".

The generic relationships of the remaining genus, Erodiophyllum, are less obvious. The genus is unique in its multiseriate pistillate florets, the outer of which are radiate and which may have 2 or 3 free stamens. The corollas of the inner pistillate florets are reduced to a densely pubescent tube less than 1.0 mm in length and are subtended by stiff, green, receptacular bracts with sharp points which become reflexed at maturity. These bracts are not present among the disk florets. Although the style branches of the sterile disk florets lack stigmatic surfaces and are fused for the greater part of their length,

Table 6. Proposed disposition of the genera of the tribe Astereae, subtribe Bellidinae.

genera of the Bellidinae	new subtribal position in the tribe Astereae
Erodiophyllum	Asterinae
Aphanostephus	Asterinae, near Townsendia, Dichaetophora, and Astranthium
Greenella	Solidagininae, with Amphipappus, Amphiachyris, Guttierrezia, Gymnosperma, and Xanthocephalum
Lagenophora	Grangeinae
Solenogyne	Grangeinae
Rhynchospermum	Grangeinae
Myriactis	Grangeinae
Achaetogeron	Asterinae, near Erigeron
Brachycome	Asterinae, near Calotis and Minuria
Bellis	Asterinae, near Bellium and Bellidiastrum
Astranthium	Asterinae, near Townsendia, and Dichaetophora

they are typically Asteroid, being glabrous on the inside and pubescent on the outside.

The well-developed cyanic rays of Erodiophyllum would suggest that the genus is a member of the subtribe Asterinae, notwithstanding the multiseriate, greatly reduced inner female florets which are reminiscent of the Grangeinae. The determination of the exact phyletic position of their genus in the Asterinae must await further study.

EXCLUDED SPECIES

Larsen (1933) placed in Astranthium species which were similar to the type species of the genus in the reduced or absent pappus, but which differed greatly not only in other floral characters, but also in vegetative characters. The taxa which are anomalous in the genus on this basis are Astranthium mimum (Blake) Larsen, A. mexicanum (A. Gray) Larsen var. mexicanum, A. mexicanum (A. Gray) Larsen var. chihuahuense Larsen, and the more recently described A. guatemalense Blake. These four taxa have the following floral characters in common: (1) A flat or slightly convex receptacle; (2) Numerous, unequal, narrow, herbaceous or subherbaceous phyllaries; (3) Numerous (more than 60) narrow-rayed pistillate florets in more than one series; (4) Oblong, two-nerved achenes which are often widest about the middle and taper off towards the base and apex. The leaves of A. mexicanum var. mexicanum are entire to coarsely toothed while those of the other taxa are entire but differ from typical members of Astranthium in shape and texture.

The floral characters listed above, together with the reduced or absent pappus, are characteristic of the genus Achaetogeron. The status of this genus was recently discussed by De Jong and Longpre (1963) and it was provisionally considered to be distinct by these authors. Pending further studies in Achaetogeron, the above taxa are best placed in that genus. The following transfers and name changes will be effective:

1. Achaetogeron guatemalensis (Blake) De Jong, comb. nov.

Astranthium guatemalense Blake, Brittonia 2: 335. 1937.

Type: GUATEMALA: in open pinewoods, along trail between Huehuetenango and Soloma, Sierra Cuchumatanes, Dept. Huehuetenango, alt. 3335 m (11,000 ft), 15 Sept 1934, Skutch 1239 (holotype, GH!; isotype, F!).

2. Achaetogeron mexicanus (A. Gray) De Jong, comb. nov.

Bellis mexicana A. Gray, Smiths. Contr. 5: 93. 1852.

Brachycome mexicana (A. Gray) Reiche, Fl. Exc.: 184. 1926.

Astranthium mexicanum (A. Gray) Larsen, Ann. Mo. Bot. Gard. 20: 32. 1933.

Type: STATE OF MEXICO: without locality, 26 April 1849, Gregg 701 (holotype, GH!; isotype, MO!).

Both A. guatemalensis ($n = 9$) and A. mexicanus ($n = 9, 18$) have chromosome numbers on a base of $x = 9$, which is also the basic chromosome number of Achaetogeron (De Jong and Longpre, 1963). A. mexicanus bears a remarkable resemblance to Achaetogeron Galeottii and A. affinis, but insufficient material of the latter two did not allow for a critical and detailed comparison of the three species. More detailed studies may show them to be conspecific.

3. Achaetogeron perennis De Jong, nom. et stat. nov.

Astranthium mexicanum (A. Gray) Larsen var. chihuahuense Larsen, Ann. Mo. Bot. Gard. 20: 32. 1933.

Type: CHIHUAHUA: canyons of the Sierra Madre (Occidental), 4 Oct 1888, Pringle 2015 (holotype, MO!; isotypes, GH!, 2 sheets; MSC!; PH!).

This taxon is sufficiently distinct from A. mexicanus in its entire leaves and glabrous achenes with a small, but conspicuous pappus crown to warrant its recognition as a species. Since an earlier Achaetogeron chihuahuensis was described by Larsen (in Blake, 1940), a new epithet has been coined.

4. Achaetogeron mimus (Blake) De Jong, comb. nov.

Bellis mima Blake, Contr. U.S. Nat. Herb. 22: 594. 1924.

Astranthium mimum (Blake) Larsen, Ann. Mo. Bot. Gard. 20: 30. 1933.

Type: DURANGO: 30 KMs N of Guanacevi, alt. 2440 m to 2745 m, 13 Aug 1898, Nelson 4786 (holotype, US!; isotype, GH!).

Achaetogeron mimus is only known from the type locality in northern Durango and is distinct in its large, obovate-oblong leaves with long, slender petioles, linear-lanceolate cauline leaves which are reduced upward, and few, large, many-flowered heads.

SYSTEMATIC TREATMENT

The herbaria from which specimens were borrowed are listed below. Abbreviations are those in the fifth edition of "Index Herbariorum" (Lanjouw and Stafleu, 1964).

Chicago Natural History Museum (F); Conservatoire et Jardin Botaniques, Geneva (G); Gray Herbarium, Harvard University (GH); University of Glasgow (GL); University of Kansas (KANU); University of Michigan (MICH); Missouri Botanical Garden (MO); Michigan State University (MSC); University of Oklahoma (OKL); Oklahoma State University (OKLA); Muséum National d'Histoire Naturelle, Paris (P); Philadelphia Academy of Natural Sciences (PH); Southern Methodist University (SMU); Sul Ross State College (SRSC); University of Texas (TEX); University of California (UC); U. S. National Museum (US); University of Wisconsin (WIS).

ASTRANTHIUM Nutt. Trans. Am. Phil. Soc. N. S. 7: 312. 1841.

Annual, biennial, and perennial, caulescent herbs with taproots, fibrous roots, or fibrous-rooted caudices; stems erect, ascending, or decumbent, striate and grooved, sparingly to densely strigose with spreading to appressed trichomes; basal leaves broadly spathulate to narrowly oblanceolate (lacking in A. xylopodum), essentially glabrous to somewhat densely appressed-strigose; cauline leaves alternate, sessile, spathulate to linear, mostly strongly reduced upward, glabrous to densely strigose, the margins entire, rarely toothed, ciliate, sometimes revolute, the apices mucronate to acuminate; heads medium-sized

to large (secondary heads often small), cernuous and subtended by the upper cauline leaves prior to anthesis, commonly long-pedunculate, the peduncles naked or with one or two small, linear, leaf-like bracts; receptacle conical, rarely low-conical, alveolate; involucre campanulate or hemispherical; phyllaries imbricated in mostly 2, rarely 3 series (sometimes a single series in secondary heads), flattened, broadly ovate to linear-lanceolate, glabrous to densely strigose on the outside, glabrous and shiny within, the margins prominently scarious, rarely near-herbaceous throughout, lacerate-ciliate mostly above the middle, the apices acute or lacerate-acuminate; ray florets pistillate, fertile, in one series, 10 - 35, white throughout, or white above and dark lavender below or the lower surface with alternating bands of dark and light lavender, the upper surface appearing light lavender when viewed from above, the tube with scattered hairs, the apices 2 - 4-dentate or -denticulate; disk florets perfect, 40 - 260, yellow, the corolla rarely slightly, but more commonly abruptly contracted at the minutely pubescent throat; anthers with apical appendages and rounded anther bases, the erectile tissue in the filaments nearly always of a bright orange color prior to anthesis, changing to pale yellow at anthesis; style branches of the disk glabrous on the inside, pubescent without, the stylar appendages ovate to ovate-lanceolate, slightly shorter than to about one and a half times the length of the stigmatic lines; achenes obovate to oblanceolate, laterally compressed, glabrous or glochidiate-pubescent with duplex, bifurcate hairs, greenish-brown to dark brown; disk and ray achenes 2-nerved or obscurely so, or conspicuously 2- or 3-ribbed, triquetrous when 3-ribbed, the faces of the ribbed achenes nerveless or with one or two prominent nerves;

pappus absent or a minute crown of a few whitish or yellowish teeth less than 0.1 mm high. Type species and originally the only species in the genus: Astranthium integrifolium (Michx.) Nutt.

Key to the Species

A. Achenes 2- or 3-ribbed, triquetrous when 3-ribbed, the achenial faces with 1 or 2 conspicuous, longitudinal nerves or nerveless, glabrous, 2.5 - 3.2 mm long; cauline leaves nearly similar in size and shape throughout; rays white; perennials ..... B

B. Plants with a stout or slender woody taproot, often with rough bark; cauline leaves 3-nerved; limb of the disk florets 3.4 - 4.1 mm long, slightly contracted at the throat; outermost phyllaries 6.0 - 8.5 mm long, ovate-lanceolate to linear-lanceolate; achenial ribs of a lighter color than the faces; achenes nerved or nerveless; pappus absent; plants from Nayarit, Jalisco, and Michoacan..... 1. A. xylopodum

B. Plants with a fibrous-rooted caudex; cauline leaves sometimes with 1 - 5 small, callous-tipped teeth; limb of the disk florets 3.3 - 3.7 mm long, abruptly contracted at the throat; outermost phyllaries 4.5 - 6.0 mm long, broadly ovate to ovate-lanceolate; achenial ribs of the same color as the nerveless faces; pappus absent or a small, whitish crown of teeth less than 0.1 mm high; plants from eastern Michoacan..... 2. A. laetificum

A. Achenes 2-nerved, never ribbed, glabrous or glochidiate-pubescent, 1.8 - 2.3 mm long, epappose or with a small, whitish or yellowish crown of teeth less than 0.1 mm high; cauline leaves strongly reduced upward in length and width; rays white, or lavender below and pale lavender above; annuals, biennials, and perennials.... C

C. Rays white, sometimes roseate in drying, but never bright blue or purple when dry ..... D

D. Plants with fibrous-rooted caudices; plants from eastern Mexico..... E

E. Erect, open-branched perennials; flowering stems numerous, branched at or below the middle; plants from San Luis Potosi, Hidalgo, Oaxaca, and Chiapas..... 3. A. purpurascens

E. Procumbent, stoloniferous perennials, the stolons basal or cauline; erect flowering stems rarely more than 1; plants from Hidalgo, Puebla, Tlaxcala, and Veracruz..... ..... 4. A. xanthocomoides

D. Plants with short or slender taproots, or if fibrous-rooted, then the lower cauline leaves narrow and less than 6.0 mm wide; plants from western Mexico..... F

F. Biennial or short-lived perennials from a short taproot or fibrous-rooted caudex, the stem-root junction often conspicuously thickened; stems erect or ascending, rarely decumbent; lower cauline leaves narrowly spathulate to oblanceolate, less than 6.0 mm wide; plants from Chihuahua and Durango..... 8. A. orthopodum

F. Annuals from a slender taproot, often with fibrous lateral roots; stems commonly decumbent, the central ones ascending; lower cauline leaves spathulate or oblanceolate to lanceolate, sometimes subulate, commonly more than 6.0 mm wide; plants from Jalisco and Michoacan..... 9. A. condimentum

C. Rays lavender, bright blue or purple when dry..... G

G. Perennials from a fibrous-rooted caudex; basal leaves mostly persistent, with long-tapering leaf bases; stems few, decumbent or ascending, simple or rarely once-branched below the middle; midrib of cauline leaves not quite extending into the apices; multiple crowns often present and the plants then matted..... H

H. Achenes evenly glochidiate-pubescent; rays lavender throughout; plants from southern Nuevo Leon and eastern Tamaulipas..... 6. A. splendens

H. Achenes glabrous, rarely sparsely glochidiate-pubescent mostly around the apex; rays lavender throughout or with alternating bands of light and dark lavender below, paler above; plants from Cerro Potosi, Nuevo Leon..... 7. A. Besmanii

G. Annuals, fibrous- or taprooted; basal leaves soon deciduous; stems erect, ascending, or decumbent, mostly (in mature specimens) much-branched below to above the middle; midrib extending into the apices of the leaves; multiple crowns never present..... I

I. Fibrous- or taprooted; stems commonly erect or ascending; cauline leaves not densely crowded; plants from northern Nuevo Leon, and the south-central and east-central United States..... ..... 5. A. integrifolium

I. Taprooted; stems mostly decumbent, with densely crowded leaves; plants from the Trans Pecos region of Texas..... 10. A. robustum

1. Astranthium xylopodum Larsen

Astranthium xylopodum Larsen, Ann. Mo. Bot. Gard. 20: 31. 1933.

Koerlia mexicana A. Gray ex S. Wats., Proc. Am. Acad. 22: 422. 1887.

Type: JALISCO: Rio Blanco , 16 July 1886, Palmer 146 (holotype, GH!; isotype, PH!).

Perennial, to 50.0 cm high, from a simple or branched, slender to stout woody taproot; stems 1 - several, erect or ascending, simple or loosely branched about the middle, greenish-brown to purplish, grooved and striate, essentially glabrous to densely strigose with coarse trichomes; peduncles 7.0 - 30.0 cm long, moderately to densely white-pubescent below the heads; basal leaves not seen and not observed in greenhouse-grown seedlings; cauline leaves nearly glabrous to evenly and densely pubescent with coarse trichomes, up to 2.0 mm long, mostly prominently three-nerved, the midrib conspicuous above and below, the margins entire, often revolute, sometimes purplish, short- or long-ciliate, the apices obtuse or mucronate; lower cauline leaves reduced in size, 0.8 - 3.0 cm long, 0.2 - 1.1 cm wide, spathulate to oblanceolate, soon shriveling; middle cauline leaves oblong, elliptic, or oblanceolate, 1.9 - 5.0 cm long, 0.5 - 1.3 cm wide, upper cauline leaves similar in shape and as large as the middle leaves or somewhat reduced, but rarely as small as the lower cauline leaves; heads 1 - 8, rarely more, large, solitary on the peduncles; receptacle low-conical; involucre campanulate, 0.5 - 1.0 cm high, 0.9 - 1.5 cm

Plate 9. Astranthium xylopodum, drawn from De Jong 1028 (MSC).

wide; phyllaries imbricated in 2 or 3 series, the outermost ovate-lanceolate to linear-lanceolate, 6.0 - 8.5 mm long, 1.0 - 2.1 mm wide, nearly herbaceous throughout or with narrow to conspicuous scarious margins, these lacerate-ciliate from below the middle to the apex, sparsely to densely pubescent on the back, glabrous and shiny within, with often purplish, acute to acuminate apices; second series linear-lanceolate, 6.0 - 8.0 mm long, 1.0 - 1.6 mm wide, glabrous to moderately pubescent on the back; innermost (third) series, if present, 5.0 - 7.0 mm long, 0.9 - 1.2 mm wide, often hyaline throughout; ray florets 15 - 30, white, sometimes roseate when dried, the corolla 1.0 - 2.1 cm long, 1.5 - 3.0 mm wide, the apex 2 - 4-dentate or -denticulate; disk florets 90 - 120, the tube 3.4 - 4.1 mm long, slightly contracted at the throat, the lobes 0.9 - 1.0 mm long; style branches of the disk with ovate or ovate-lanceolate appendages, about as long to one and a half times as long as the stigmatic lines; ray and disk achenes obovate, 2.5 - 3.2 mm long, 1.4 - 1.7 mm wide, with conspicuous ribs, the achenial faces nerveless or with 1 or 2 conspicuous nerves, glabrous, shiny, greenish-brown (with yellowish ribs and nerves) or dark-brown (with light-brown ribs and nerves), the ray achenes 2- or 3-ribbed (triquetrous when 3-ribbed), the disk achenes 2-ribbed or those nearest the rays often 3-ribbed and then triquetrous; pappus absent; chromosome number $\underline{n} = 5$, as determined from PMC squashes. Plate 9.

Distribution: Western Mexico, at elevations between 800 and 1500 meters in the Sierra Madre Occidental, in the states of Nayarit, Jalisco, and Michoacan, in oak forests at lower elevations and pine-oak forests at higher elevations. Principal flowering dates from

June to August. Plate 11.

Specimens examined:

JALISCO: pine-oak forest, Sierra del Halo, near lumber road to San Isidro, elev 1490 m, 12 Aug 1961, De Jong 1028 (GH; MSC; TEX; UC; US); in pine forest, Sierra del Halo, near lumber road to San Isidro, elev 1530 m, 14 Aug 1957, McVaugh 16167 (MICH; MSC); Rio Blanco , 16 July 1886, Palmer 146 (holotype, GH!; isotype, PH!); shaded hillsides near Guadalajara, 27 June - 14 July 1893, Pringle 4412 (F; GH; MICH; MO; MSC; PH; UC). MICHOACAN: oak forest, Coalcoman, distr. Coalcoman, elev 1250 m, 16 July 1939, Hinton 13959 (GH; MO; PH; US).

NAYARIT: oak forest along Hwy from Tepic to Compostela, 7.5 mi N of Compostela, elev 800 m, 10 Aug 1961, De Jong 1013 (MSC); loam soil, wooded slopes and barrancas leading down to lake NE of Santa Maria del Oro, elev ca 1000 m, 18 - 20 Aug 1959, Feddema 634 (MICH); pine forests in mountains, ca 35 mi SW of Jalisco, road to El Malinal, elev 1150 - 1200 m, 19 June 1957, McVaugh 14922 (MICH); red clay hills, oak forest zone, 7 mi N of Compostela, elev 800 - 850 m, 11 July 1957, McVaugh 15303 (MICH).

The primitive characters of Astranthium xylopodum are discussed in greater detail in the section on the evolution of the genus. The species is unique in Astranthium in its large, prominently ribbed and often nerved achenes, leaves which are hardly reduced upward, and woody taproot. Astranthium xylopodum requires relatively dry habitats in oak-, pine-oak-, or pine-forests at elevations which are the lowest for any species of Astranthium. Its requirements of red clay soils

parallel those of several other species in the genus.

Astranthium xylopodum is somewhat variable in pubescence. The type collection, Palmer 146, and Pringle 4412, both from Jalisco, and the Hinton 13959 specimens from Michoacan are moderately to densely pubescent with coarse trichomes up to 2.0 mm long. On the other hand, all other specimens examined were essentially glabrous or sparsely pubescent with trichomes which are shorter and less coarse.

The closest relationship of A. xylopodum is with A. laetificum. Both species have chromosome numbers on a base of $x = 5$ and their karyotypes show many similarities. The achenes of A. laetificum are very similar to those of A. xylopodum and the two species resemble one another in habit and leaf characters. Also, the distribution pattern of the two species, when correlated with morphological and cytological characters, indicates a close relationship. Astranthium laetificum differs from A. xylopodum, however, in its fibrous-rooted caudex, reduced phyllaries, abruptly contracted disk florets, and tetraploid chromosome number.

2. Astranthium laetificum De Jong, sp. nov.

Type: MICHOACAN: in Pinus-Abies forest area, Route 15, between KMs 246 and 247, 1.5 mi W of Mil Cumbres, elev 2490 m, 17 Aug 1961, De Jong 1104 (Holotype: MSC!; isotypes, GH!; TEX!; UC!; US!).

Perennis, caulibus simplicibus vel ramosis, ascendentibus vel decumbentibus, ad 35.0 cm altis, pubescentibus pilis patentibus vel adpressis; folia basilaria spathulata, integra vel 1 - 5-serrata; folia caulina integra vel 1- 5-serrata, intermedia spathulata ad oblanceolata, 2.2 - 6.0 cm longa, 0.5 - 1.5 cm lata, superiora pauci-reducta, suprema breve spathulata ad plus minusve linearia, 1.4 - 4.2 cm longa, 0.3 - 0.9 cm lata; pedunculi circa 6.0 - 25.0 cm longi, nudi vel cum bracteis solitariis, linearibus et minutis; capitula solitaria, involucris 0.45 - 0.60 cm altis, 0.9 - 1.3 cm latis; phyllaria 2- vel 3-seriata, aequalia, late ovata ad ovato-lanceolata, apice acuta vel longe acuminata, scarioso-marginata; flores radii circa 15 - 25, 1-seriati, albi; flores disci circa 80 - 110, corollis 3.3 - 3.7 mm longis, flavis; achaenia disci et radii obovata ad oblanceolata, 2.5 - 3.5 mm longa, 1.0 - 1.5 mm lata, compressa, glabra, sine pappo vel cum corona papposa minutissima; achaenia disci 2-costata, sed tamen achaenia radii 2- vel 3-costata; chromosomarum n = 10.

Perennial, to 35.0 cm high, from a simple or branching, vertical, oblique, or horizontal, fibrous-rooted caudex; stems 1 - several (rarely as many as 12), decumbent, ascending, or erect, simple or loosely branched below the middle, greenish to purple, sparsely to

Plate 10. *Astranthium laetificum*, drawn from *De Jong 1104* (MSC).

moderately strigose; peduncles 6.0 - 25.0 cm long, naked or with a single, minute linear bract, the summits moderately to densely pubescent below the heads; basal leaves spathulate, sparsely to moderately pubescent above and below, becoming glabrous toward the long-tapering base, the margins short-ciliate and sometimes revolute, entire or sometimes with 1 - 5 callous-tipped teeth, the apices obtuse or mucronate; cauline leaves sparsely pubescent above and below, glabrous toward the base, the margins short-ciliate, entire, or with 1 - 5 small, callous-tipped teeth, the apices mucronate; lower cauline leaves shriveling and soon wanting, spathulate, 1.4 - 4.5 cm long, 0.3 - 1.2 cm wide, the middle cauline leaves spathulate to oblanceolate, 2.2 - 6.0 cm long, 0.5 - 1.5 cm wide, the uppermost short-spathulate to nearly linear, mostly reduced, 1.4 - 4.2 cm long, 0.3 - 0.9 cm wide; receptacle conical; involucre campanulate to hemispherical, 4.5 - 6.0 mm high, 0.9 - 1.3 cm wide; heads 1 - 8 (-12), solitary on the peduncles; phyllaries imbricated in 2 series, rarely with a third, innermost series, about equal in length, 4.5 - 6.0 mm long, 1.2 - 2.5 mm wide, broadly ovate to ovate-lanceolate, the margins scarious, lacerate-ciliate above the middle, often purplish, the green midportion densely pubescent on the back, the apices acute to long-acuminate; innermost (third) series, if present, linear-lanceolate, with very narrow midportion and conspicuous scarious margins or hyaline throughout; ray florets 15 - 25, white or sometimes somewhat roseate near the 2- or 3-toothed apex; disk florets 80 - 110, the tube 3.3 - 3.7 mm long, strongly contracted at the throat, the lobes ca. 1.0 mm long; stamens with subulate apical appendages and rounded anther bases; style branches of the disk with narrowly ovate appendages

about as long to one and a half times as long as the stigmatic lines; achenes obovate to oblanceolate, 2.5 - 3.5 mm long, 1.0 - 1.5 mm wide, glabrous, shiny, greenish-brown to golden-brown, 2-ribbed or the ray achenes often 3-ribbed, the ribs of the same color as the achenial faces, the faces sometimes with a superficial ridge; pappus absent or a minute whitish crown less than 0.1 mm high; chromosome number n = 10, determined from PMC squashes. Plate 10.

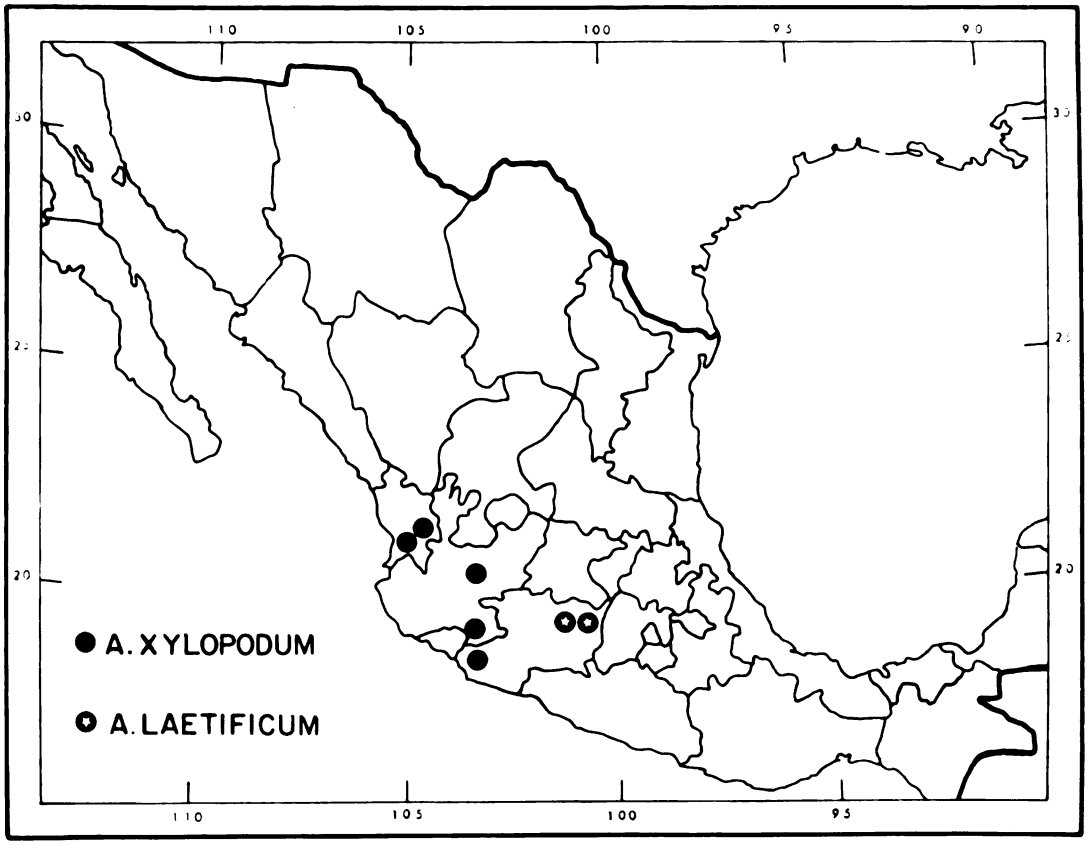
Distribution: in the mountains of the Transvolcanic Belt in eastern Michoacan, in pine-fir forest at ca. 2500 meters elevation. Known only from the type locality and one additional locality near Morelia. Flowering in August. Plate 11.

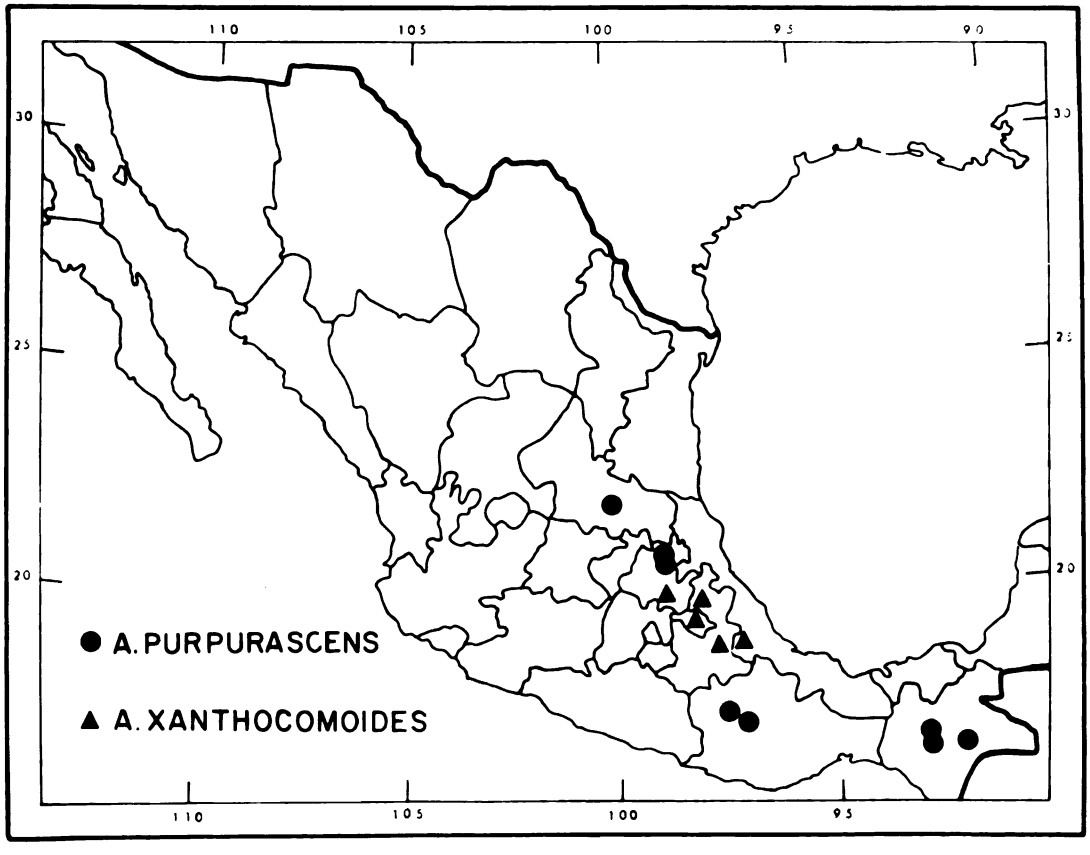
Additional specimen examined:

Morelia, June-October, 1840, Galeotti 2420 (P).

The similarities between A. laetificum and A. xylopodum are indicated in the discussion of the latter. In addition to being related to A. xylopodum, A. laetificum is also related to A. purpurascens on the basis of the perennial habit, fibrous-rooted caudex and open branching habit. However, the leaves of A. purpurascens are more numerous and are lighter in color and texture than those of A. laetificum. Also, the heads of A. purpurascens are usually more numerous and the achenes are 2-nerved, never ribbed. In addition, A. laetificum is a tetraploid on a base of x = 5 whereas A. purpurascens is a tetraploid on a base of x = 4. Through A. laetificum, it is possible to recognize the relationships of A. xylopodum with the remaining species of Astranthium.

Plate 11. Geographic distribution of A. xylopodum, A. lactificum, A. purpurascens, and A. xanthocomoides.


110
105
100
95
90
30
25
20
A. XYLOPODUM
A. LAETIFICUM


110
105
100
95
90
30
25
20
A. PURPURASCENS
A. XANTHOCOMOIDES

3. Astranthium purpurascens (Robins.) Larsen

Astranthium purpurascens (Robins.) Larsen, Ann. Mo. Bot. Gard. 23: 33. 1933.

Bellis purpurascens Robins., Proc. Am. Acad. 27: 172. 1892.

Type: SAN LUIS POTOSI: shaded grassy slopes, Barranca of Las Canoas, 18 Aug 1891, Pringle 3819 (holotype, GH!; isotypes, F!; GH!; MO!, 2 sheets; MSC!; PH!, 2 sheets; UC!; US!).

Perennial, to 60.0 cm high, from a short, vertical, simple or somewhat branched, fibrous-rooted caudex; stems 1 - numerous, simple or repeatedly branched at or below the middle, erect or ascending, rarely decumbent, greenish to reddish-purple, glabrous to densely strigose with spreading hairs; peduncles to 20.0 cm long, the summits sparsely to densely white-pubescent below the heads; basal leaves spathulate to narrowly so, deciduous or persistent, essentially glabrous or sparsely to moderately pubescent throughout above and below, or the upper surface sparsely to moderately pubescent above the middle and toward the apex and then glabrous toward the base, the lower surface similar to the upper or pubescent on the midrib only, the margins nearly glabrous to moderately ciliate-pubescent, the apices obtuse or mucronate; lower cauline leaves often shriveling, spathulate to lanceolate or oblanceolate, 0.9 - 5.0 cm long, 0.2 - 1.8 cm wide, rarely longer and wider, the upper surface essentially glabrous to densely pubescent above the middle and then glabrous toward the base or glabrous to densely pubescent throughout, the lower surface glabrous

Plate 12. *Astranthium purpurascens*, drawn from *De Jong 1227* (MSC).

or sparsely pubescent throughout, or sparsely pubescent only above the middle and then glabrous toward the base except for the pubescent midrib; middle and upper cauline similar to the lower in characters of pubescence, the middle cauline leaves spathulate, ovate, obovate, or lanceolate to lance-elliptic, 0.7 - 5.8 cm long, 0.2 - 1.7 cm wide, the apices minutely mucronate, cuspidate, or acuminate; upper cauline leaves lanceolate, lance-elliptic, or linear-lanceolate, 0.5 - 2.8 cm long, 1.0 - 8.8 mm wide, the apices cuspidate to long-acuminate; receptacle conical, becoming steeply so at maturity; heads 1 - numerous, small to large, solitary on the peduncles; involucre campanulate, 3.0 - 7.2 mm high, 0.7 - 1.7 cm wide; phyllaries imbricated in 2, rarely in 1 or 3, about equal series, broadly ovate to lanceolate, linear-lanceolate or oblanceolate, 3.0 - 7.2 mm long, 0.9 - 2.1 mm wide, with conspicuous to narrow, often pinkish to purplish scarious margins, these lacerate-ciliate mostly above the middle, the green midportions of the phyllaries glabrous to sparsely pubescent on the back, the apices ciliate-acuminate; ray florets 10 - 30, white, the lamina 0.9 - 1.4 cm long, 2.0 - 3.0 mm wide, the apices 2- or 3-denticulate or -dentate, or conspicuously 2- or 3-cleft; disk florets 40 - 155, the tube contracted at the throat, 2.1 - 3.7 mm long, the lobes 0.7 - 0.9 mm long; stylar appendages of the disk ovate to ovate-lanceolate, half to about one and a half times the length of the stigmatic lines; achenes obovate, glabrous to sparsely glochidiate-pubescent, compressed or hardly so, 1.5 - 2.3 mm long, 0.8 - 1.2 mm wide, conspicuously or obscurely 2-nerved, greenish-brown to reddish-brown, sometimes reddish-purple around the apex; pappus absent or a minute yellowish crown with a few teeth less than 0.1 mm high; chromosome number $n = 8$, determined

from PMC squashes. Plate 12.

Distribution: in the Sierra Madre Oriental, in the states of San Luis Potosi and Hidalgo, and in the mountains of Oaxaca and Chiapas, occurring principally between 1700 and 2300 meters elevation. Habitats are open pastures, open pine forests, pine-oak-juniper stands, oak forests, or oak-cypress woodland. Principal flowering dates from June through November. Plate 11.

Specimens examined:

CHIAPAS: open pine-oak-juniper stand, 9 mi NW of Comitan, elev 1790 m, 28 Aug 1961, De Jong 1146 (GH; MSC; TEX; UC; US); moist open pasture at San Nicolas, 5.2 mi SE of Teopisca, elev 1820 m, 25 Aug 1961, De Jong 1164 (GH; MSC; TEX; UC; US); without locality or date, Ghiesbreght 135 (GH; P); without locality, 1864 - 1870, Ghiesbreght 548 (GH; MO); mountains along Route 190, about 5 mi E of San Cristobal de las Casas, 11 June 1960, King 2803 (MICH; TEX; UC); wet fields, just W of San Cristobal de las Casas, 24 June 1960, King 2996 (MICH; MSC; TEX; UC); pine-oak forest, about 10 mi E. of Teopisca, 24 June 1960, King 3011 (MICH; MSC; TEX; UC); sandy loam, pine-oak forests, in mountains along Route 190, about 9 mi NW of Comitan, 25 June 1960, King 3056 (MICH; MSC; TEX; UC). HIDALGO: mountain side, Jacala, elev 4500 ft, 25 June 1939, Chase 7131 (F); rocky ravine, Jacala, elev 5000 ft, 5 July 1939, Chase 7322 (F; GH; MICH; MO); steep, N-facing, pine-forested slope at village limit of Cobrecito, between KMs 236 and 237, Route 85 elev 2130 m, 5 Sept 1961, De Jong 1227 (GH; MSC; TEX; UC; US); mountainous area in open Oak-Taxodium grased woodlands, 6.7 mi S of Jacala, on Route 87, 28 July 1959, Rock M-310

(TEX). OAXACA: limestone slope along Route 190, between KMs 412 and 413, elev 2130 m, 23 Aug 1961, De Jong 1131 (GH; MSC; TEX; UC; US); on grassy slope at edge of oak forest, red clay loam, between KMs 484 and 485, Route 190, 0.2 mi W of El Fortin, elev 2220 m, 30 Aug 1961, De Jong 1176 (GH; MSC; TEX; UC; US). SAN LUIS POTOSI: shaded grassy slopes, Barranca of Las Canoas, 18 Aug 1891, Pringle 3819 (holotype, GH!; isotypes, F!; GH!; MO!, 2 sheets; MSC!; PH!, 2 sheets; UC!; US!); without locality, 1891, Virlet d'Aoust 342 (P); without locality, 1891, Virlet d'Aoust 449 (P).

The range of Astranthium purpurascens is made up of three populations separated from one another by considerable distances. The northernmost of these populations is in the Sierra Madre Oriental in the states of San Luis Potosi and Hidalgo. The second population is in the mountains of Oaxaca and is separated from the first by a distance of some 300 miles. The Oaxaca population is in turn separated from the third population in Chiapas by a distance of about 250 miles.

The plants of the three populations differ especially in characters of pubescence, but these characters are too intangible to be of value in the separation of the plants. Thus, the Chiapas plants are essentially glabrous to sparsely pubescent and the achenes are mostly glabrous, rarely with a few glochidiate hairs. Contrariwise, the Oaxaca plants are sparsely to densely pubescent and the achenes are mostly sparsely glochidiate-pubescent. The San Luis Potosi and Hidalgo plants are, on the whole, less pubescent than the Oaxaca plants but the achenes are glabrous or sparsely glochidiate-pubescent like those of the Chiapas plants. The three populations are similar

in all other characters and their karyotypes are also similar. On this basis, it seems best to recognize Astranthium purpurascens as a single, if somewhat polymorphic species.

Although the three populations are homoploid and belong to the same species, crosses between plants of the three populations yielded highly sterile hybrids. Details on these crosses may be found in the section on crossing relationships in the genus.

The relationships of Astranthium purpurascens are with A. laetificum and with A. integrifolium. The similarities with the latter were recognized by Larsen (1933). Astranthium integrifolium, however, is well set apart by the annual habit, smoother leaves, more numerous heads, and lavender rays. Their genetic kinship is indicated by the fact that both species have chromosome numbers on a base of $x = 4$.

A. purpurascens is also related to A. xanthocomoides. Although distinct from A. purpurascens in its stoloniferous habit, and considerably narrower leaves, A. xanthocomoides shares the same level of ploidy ($n = 8$), and both species have the smallest somatic chromosome pair with satellites.

4. Astranthium xanthocomoides (Less.) Larsen

Astranthium xanthocomoides (Less.) Larsen, Ann. Mo. Bot. Gard. 20: 33. 1933.

Brachycome xanthocomoides Less. Syn. Comp. 192. 1832.

Brachycome xeranthocomoides Steud. Nomencl. Bot. 2: 220. 1840. (typographical error).

Bellis xanthocomoides A. Gray ex Hemsley, Biol. Centr. Am. Bot. 2: 118. 1881.

Type: VERACRUZ: Prope La Jaya (La Hoya) , 29 June, Schiede 206 (holotype, not known, possibly in HAL ; isotype, MO!).

Perennial, to 25.0 cm high, from a slender, fibrous-rooted caudex with mostly one erect flowering stem and few to many ascending or decumbent flowering stems and stolons; flowering stems 1 - many, simple or branched, green to purplish, sparsely to moderately strigose; stolons few to many, simple or branched, similar to the flowering stems in pubescence and often bearing capitula; basal leaves soon deciduous, narrowly oblanceolate or spathulate, to 4.0 cm long and ca 1.0 - 1.7 cm wide, the blade nearly glabrous to moderately pubescent above and below, often glabrous toward the base, the margins ciliate, the apices mucronate; lower cauline leaves narrowly spathulate or oblanceolate, glabrous to moderately pubescent above and below and then often toward the base, the margins ciliate, the apices prominently mucronate; middle and upper leaves gradually reduced in size and similar to the lower cauline leaves in characters of pubescence, the uppermost

Plate 13. *Astranthium xanthocomoides*, drawn from *De Jong 1195* (MSC).

narrowly oblanceolate to linear-lanceolate, the apices long-acuminate; stolons basal, and then procumbent, or cauline, up to 40.0 cm long, with narrowly spathulate to linear-lanceolate, often minute (less than 5.0 mm long) leaves, the tips of the stolons terminating in a capitulum or in a leafy rosette, the latter taking root and forming a new plantlet; peduncles to 12.0 cm long, naked, or with a minute, linear-lanceolate bract; heads 1 - few, borne singly on stems or stolons; receptacle conical; involucre campanulate, 4.2 - 7.2 mm high, 0.8 - 1.5 cm wide; phyllaries imbricated in two equal series, 4.2 - 7.2 mm long, 1.0 - 1.8 mm wide, obovate to narrowly lanceolate, glabrous to sparsely pubescent on the back, the scarious margins lacerate-ciliate mostly above the middle, often purplish, the apices ciliate-acuminate; ray florets 15 - 26, white, sometimes roseate before anthesis and in drying, the lamina 0.9 - 1.4 cm long, 2.4 - 3.0 mm wide, the apex entire or 2 - 3-toothed; disk florets 60 - 120, the limb contracted at the throat, 2.5 - 3.3 mm long, the lobes 0.6 - 0.8 mm long; anthers with minute subulate apical appendages; stylar appendages of the disk narrowly ovate, about as long to three quarters as long as the stigmatic lines; achenes obovate or narrowly so, 1.4 - 2.0 mm long, 0.7 - 1.0 mm wide, greenish-brown to dark-brown, nearly glabrous to moderately glochidiate-pubescent; pappus absent; chromosome number $\underline{n}$ = 8 determined from PMC squashes. Plate 13.

Distribution: in the mountains of Hidalgo southward into the eastern mountains of the Transvolcanic Belt in Puebla, Tlaxcala, and Veracruz, principally at elevations between 2500 and 3000 meters. Habitats include moist, cool, open meadows and open pine- or fir

forests at high elevations and open pine-oak-juniper forest at lower elevations. Principal flowering dates from April through October, with a single collection obtained in February. Plate 11.

Specimens examined:

HIDALGO: ridge, ca 2 KMs S of Real del Monte, elev ca 2880 m, 7 July 1959, Beaman 2737 (MSC); without locality or date, Ehrenberg 414 (P), and Ehrenberg 616 (P); open, grassy spots, between Pachuca and Real del Monte, elev 2700 m, 27 Aug 1944, Goodman 3407 (F; OKL); open meadow in fir forest near Zerezo and below Parque Nacional El Chico, elev 3000 m, 17 Oct 1946, Moore 1550 (GH); meadows of Sierra Pachuca, elev 9000 ft, 17 - 28 July 1898, Pringle 6888 (F; GH; MO; MSC; PH; UC; US); alpine meadows, Sierra de Pachuca, elev 9500 ft, 26 Aug 1902, Pringle 9858 (F; GH; MO); moist meadows and open woods, Pachuca, July 1905, Purpus 1344 (F; GH; MO; UC); Sierra de Pachuca, 21 & 22 July 1901, Rose 5592 GH). PUEBLA: pine-oak-juniper forest and grassy roadside, 5.3 mi SW of San Salvador El Seco, elev ca 2500 m, 13 July 1960, De Jong 630 (GH; MSC; TEX; UC; US); on grassy slope at edge of pine forest, Route 119, 1.3 mi N of Tlaxcala state line, elev ca 2800 m, 2 Sept 1961, De Jong 1206 (MSC); Cerro Azul, Feb 1909, Nicolas s. n. (F). TLAXCALA: cool, moist, open meadows, Route 119, 2.2 mi S of Puebla state line, elev 2840 m, 2 Sept 1961, De Jong 1195 (GH; MSC; TEX; UC; US). VERACRUZ: among dry turf or in cultivated fields, Lomogrande, Mount Orizaba, elev 9700 ft, 27 April 1938, Ballis 4372 (UC; US); Joya, July 1841, Liebmann 507 (P, 2 sheets); Prope La Jaya (La Hoya) , 29 June, Schiede 206 (holotype, not known, possibly in HAL ; isotype, MO!).

Larsen (1933) indicated Lessing's name to be a "nomen subnudum" but the brief description of the species is valid. Lessing (1832) noted the collector as "Schiede", without locality or number, but in the emended description of the species by von Schlechtendal (1835), the locality and date are cited as "Pr. la Jaya Jun. 29". These data fit Schiede 206 in MO which is considered to be an isotype.

Astranthium xanthocomoides is a very distinctive species because of its conspicuous procumbent stolons and reduced number of capitula. Morphologically, its closest relative is A. purpurascens with which it also agrees in chromosome number and details of the karyotype. The distribution of the two species also indicates a close kinship.

5. Astranthium integrifolium (Michx.) Nutt.

Astranthium integrifolium (Michx.) Nutt., Trans. Am. Phil. Soc. N. S. 7: 312. 1841.

Key to the subspecies:

Fibrous-rooted, sometimes indistinctly tap-rooted; achenes 1.6 - 2.2 mm long, 0.9 - 1.1 mm wide, glabrous or sometimes sparsely glochidiate-pubescent about the apex; involucre 4.0 - 6.0 mm high, 1.0 - 1.5 cm wide; limb of the disk florets 2.0 - 3.2 mm long; ray corollas 1.2 - 1.5 cm long..... 5a. subsp. integrifolium

Tap-rooted, sometimes with fibrous secondary roots; achenes 1.0 - 1.6 mm long, 0.6 - 0.8 mm wide, sparsely to densely and evenly glochidiate-pubescent; involucre 2.5 - 4.5 mm high, 0.5 - 1.2 cm wide; limb of the disk florets 1.5 - 2.3 mm long; ray corollas 0.65 - 1.2 cm long.....5b. subsp. ciliatum

5a. Astranthium integrifolium (Michx.) Nutt. subsp. integrifolium.

Bellis integrifolia Michx., Fl. Bor. Am. 2: 131. 1803.

Type: TENNESSEE: "In mense maio floret Cumberland", 1795, Michaux s. n. (holotype: P , photo, MSC!; cf. discussion in the historical account of Astranthium).

Bellis parviflora Raf., New Fl. N. Am. 2: 23. 1837. Type: unknown. Locality: "Kentucky".

Bellis nutans Raf., New Fl. N. Am. 2: 23. 1837. Type: unknown.

Locality: "West Kentucky".

Bellis integrifolia Michx. var. pumila Raf., New Fl. N. Am 2: 24. 1837. Type: unknown. Locality: unknown.

Bellis integrifolia Michx. var. elata Raf., New Fl. N. Am. 2: 24. 1837. Type: unknown. Locality: unknown.

Bellis integrifolia Michx. var. carnea Raf., New Fl. N. Am. 2: 24. 1837. Type: unknown. Locality: unknown.

Annual, to 45.0 cm high, fibrous-rooted or sometimes tap-rooted but then with numerous secondary roots; stems 1 - numerous, erect, ascending, or sometimes spreading, simple or loosely branched from below to well above the middle, essentially glabrous to moderately strigose with fine, appressed and spreading trichomes, often densely pubescent toward the base, greenish to reddish-purple; peduncles to 20.0 cm long, sparsely to densely pubescent below the heads; basal leaves narrowly to broadly spathulate, 1.8 - 8.0 cm long, 0.6 - 2.2 cm wide, with long-tapering bases, the lamina sparsely pubescent above with fine trichomes, especially on the upper half and then glabrous toward the base, glabrous below or only with a few scattered hairs on the prominent midrib, the margins finely ciliate, the apices obtuse or mucronate; cauline leaves reduced upward, sparsely pubescent above, especially toward the apex and then glabrous toward the base, glabrous below or with scattered hairs on the midrib; lower cauline leaves spathulate, oblanceolate, or lanceolate, 2.3 - 5.8 cm long, 0.6 - 1.7 cm wide, the margins ciliate, the apices mucronate; middle cauline leaves elliptic to lanceolate or oblanceolate, 1.5 - 5.5 (-6.7)cm long, 0.3 - 1.5 (-2.1) cm wide, the midrib sparsely to

moderately pubescent below, the margins and apices similar to those of the lower cauline leaves; upper cauline leaves oblanceolate to lanceolate or linear-lanceolate, 0.8 - 3.6 cm long, 0.1 - 1.2 cm wide, sometimes glabrous throughout, the margins ciliate, the apices acute or acuminate; heads 1 - numerous, borne singly on the peduncles; receptacle conical; involucre campanulate to hemispherical, 4.0 - 6.0 mm high, 1.0 - 1.5 cm wide; phyllaries imbricated in two equal series or in a single series in small, secondary heads, 4.0 - 6.0 mm long, 1.0 - 2.0 mm wide, ovate or ovate-lanceolate to linear-lanceolate, the margins scarious, lacerate or lacerate-ciliate mostly above the middle, the green midportion glabrous or with a few scattered trichomes on the back, the apices acuminate to long-acuminate; ray florets 14 - 30, white or more commonly lavender below and pale above, fading in age, drying purplish-blue or dark-blue, especially on the distal half, the corolla 1.2 - 1.5 cm long, 3.0 - 4.6 mm wide, the apex entire or 2- or 3-toothed; disk florets 100 - 210, the limb 2.0 - 3.2 mm long, abruptly contracted at the throat, the lobes ca 0.5 mm long; stylar appendages of the disk ovate, about as long to one and a half times as long as the stigmatic lines; achenes obovate, 1.6 - 2.2 mm long, 0.9 - 1.1 mm wide, glabrous or sparsely glochidiate-pubescent mostly about the apex, often within the same capitulum, greenish-brown or dark brown; pappus absent or a small, whitish or yellowish crown less than 0.1 mm high; chromosome number $\underline{n} = 4$, determined from PMC squashes.

Distribution: from central Kentucky south to central Tennessee, extreme northwestern Georgia and northeastern Alabama, west into Missouri and Arkansas where it hybridizes with subsp. ciliatum. A

single collection has been obtained in central Mississippi. Principal flowering dates from May through July. Plate 14.

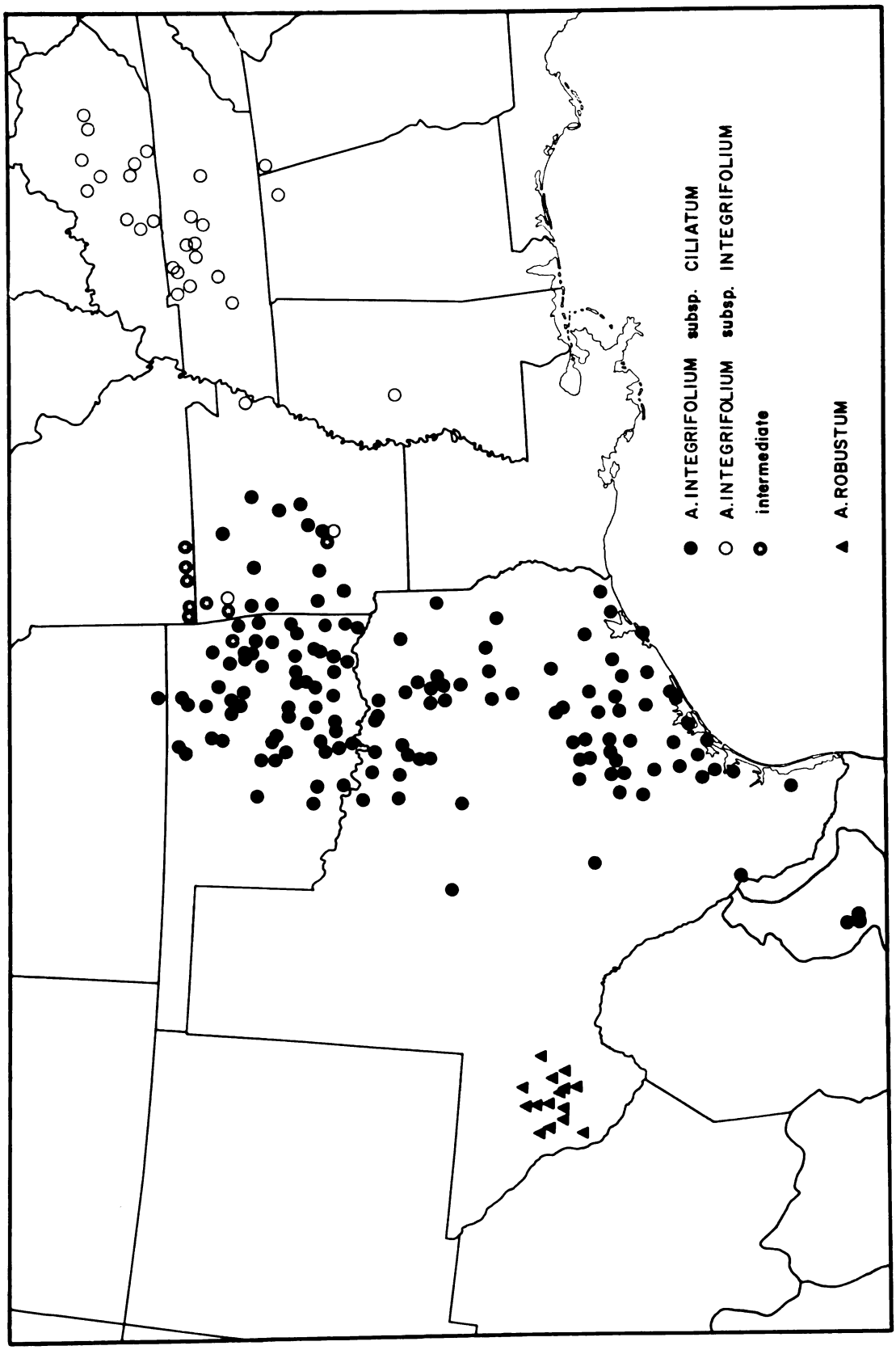
Representative specimens:

ALABAMA: JACKSON CO.: rocky banks in the mountains, Scottsboro, 2 May 1889, Mohr 41 (MSC). ARKANSAS: HOT SPRINGS CO.: Hot Springs, May 1879, Soulard s. n. (MO 122885). MISSISSIPPI CO.: Joiner, 11 June 1931, Pyle 669 (TEX). WASHINGTON CO.: Fayetteville, 1880, Harvey s. n. (MO 122880). GEORGIA: DADE CO.: dry limestone ridges near Trenton, 20 May 1899, Biltmore Herbarium No 1608b (GH); dry grounds, Ringold Road, Chickamauga, 27 May 1911, Churchill 799 (GH; MO, 2 sheets; TENN). KENTUCKY: ADAIR CO.: alluvial field, near Green River, 10 mi N of Columbia, 1 May 1959, Gibson & Watson 307 (F). ALLEN CO.: roadside at edge of woods, in dry ground, Adolphus, 21 May 1933, Weatherby & Weatherby 6351 (GH; TENN). EDMONDSON CO.: vicinity of Mammoth Cave, May 1899, Palmer s. n. (GH). ESTILL CO.: Irvine, June 1834, Peter s. n. (MICH). MADISON CO.: fields and roadsides, between Big Hill and Kingston, 9 May 1939, Braun 2385 (F); Big Hill, and the valley below it, in meadows, 1 June 1833, Short s. n. (PH); bank of creek, 1.75 mi NE of Big Hill, 17 May 1944, Wharton 6207 (TENN). MARION CO.: low ground near Buckhorn Creek, 6 mi SW of Lebanon, 9 May 1931, Wharton 3781 (TENN). MERCER CO.: damp soil, wooded flats of the Dicks River, Burgin, 10 June 1916, King 94 (F). NELSON CO.: limestone soil, edge of thickets, Balltown, 18 May 1940, Braun 2972 (F); in woods, St. Thomas, 10 May 1934, Sister Rose Agnes 1252 (MICH; UC); dry roadside near Balltown, 22 May 1933, Weatherby & Weatherby 6369 (GH). RUSSELL CO.: along roadside under oak-gum-sourwood, about 5 mi N of Russell

Springs, June 1961, Watson 173 (F). WARREN CO.: Barren River, banks, May 1890, Price s. n. (drawing, MO 122883); Bowling Green, 6 May 1892, Price s. n. (MO 122882); river bluffs, Bowling Green, May 1896, Price s. n. (MICH). WAYNE CO.: low grassy bank of Beaver Creek, SW of Monticello, 12 - 14 July 1937, Smith & Hodgdon 3912 (F; GH). MISSISSIPPI: HOLMES CO.: Tchula, 18 April 1927, Woodson & Anderson 1555 (MO). TENNESSEE: CHEATHAM CO.: wooded cove of bluffs, Harpeth River, along Route 70 S, ca 18 mi SW of Nashville, 8 May 1958, Burnett s. n. (SMU); low woods, Pegram, 6 May 1939, Svenson 10209 (GH; UC). DAVIDSON CO.: calcareous bluffs of Harpeth River, ca 15 mi SW of Nashville, 11 May 1958, Channell 7237 (SMU); limestone slope W of Nashville, 17 May 1934, Harger 7814 (GH; TENN); open cedar woods, without locality, 3 June 1923, Pennell 11441 (PH); moist field, Joelton, 16 July 1922, Svenson 118 (GH). DECATUR CO.: without locality, May 1853, Ames s. n. (MICH). HICKMAN CO.: moist, roadside ravine, between Graham and Munnelly, 20 April 1949, Sharp et al. 11869 (TENN). HOUSTON CO.: meadow near Wells Creek, Erin, 18 May 1934, Harger 7832 (GH: TENN). MONTGOMERY CO.: Dunbar Cave, 25 April 1942, Shanks 1854a (TENN); Cunningham Lake, 8 mi SW of Clarksville, 1 May 1948, Clebsch AP 119 (TENN). RUTHERFORD CO.: off US Routes 41 and 70 S, ca 4 mi N of Lavergne, 18 May 1958, Channell 7242 (SMU). STEWART CO.: near Dover, 8 May 1942, Jobe 1966 (TENN). WILSON CO.: rocky glade, Cedar of Lebanon State Park, 10 mi S of Lebanon, 11 May 1941, Kriebel 9425 (SMU). WHITE CO.: open woods and roadside, near Sparta, 13 May 1933, Weatherby & Weatherby 6277 (GH).

COUNTY UNKNOWN: "In mense maio floret Cumberland", Michaux s. n. (holotype: P , photo MSC!).

Plate 14. Geographic distribution of Astranthium integrifolium subsp. integrifolium, A. integrifolium subsp. ciliatum, and A. robustum.


A. INTEGRIFOLIUM subsp. CILIATUM
A. INTEGRIFOLIUM subsp. INTEGRIFOLIUM
intermediate
A. ROBUSTUM

5b. Astranthium integrifolium (Michx.) Nutt. subsp. ciliatum (Raf.) De Jong, stat. nov.

Bellis ciliata Raf., New Fl. N. Am. 2: 24. 1837. Type: TEXAS: "San Felipe de Austin", 1835, Drummond 221 (lectotype, NY!, photo, MSC!; isotypes, GH!; GL!; K ; NY!).

Bellis ciliata Raf. var. triflora Raf., New Fl. N. Am. 2: 25. 1837. Type: unknown. Locality: "Texas".

Astranthium integrifolium (Michx.) Nutt. var. ciliatum (Raf.) Larsen, Ann. Mo. Bot. Gard. 20: 31. 1933.

Astranthium integrifolium (Michx.) Nutt. var. rosulatum Larsen, Ann. Mo. Bot. Gard. 20: 36. 1933. Type: TEXAS: Matagorda Co.: on sandy prairies, Matagorda, 5 March 1914, Palmer 4855 (holotype, MO!).

Annual, to 30.0 cm high, with a taproot or sometimes with fibrous secondary roots; stems 1 - numberous, erect or ascending, simple or loosely branched from below to above the middle, glabrous to sparsely strigose, often densely strigose near the base, greenish to reddish-purple; peduncles to 10.0 cm long, sparsely to densely pubescent below the heads; basal leaves narrowly spathulate, 1.2 - 5.4 cm long, 0.5 - 1.3 cm wide, sparsely pubescent above, especially toward the apex and then glabrous toward the base, glabrous below or with a few scattered hairs, the margins ciliate, the apices obtuse or mucronate; cauline leaves reduced upward, sparsely to moderately pubescent above or only so toward the distal end and then glabrous toward the base, glabrous or sparsely to moderately pubescent on the midrib below, the

margins ciliate; lower cauline leaves narrowly spathulate to oblanceolate, 1.5 - 4.0 cm long, 0.4 - 1.2 cm wide, the margins often purplish, the apices mucronate; middle cauline leaves similar in shape, 0.6 - 2.7 cm long, 1.6 - 7.0 mm wide, the apices mucronate; upper cauline leaves narrowly lanceolate to linear-lanceolate, 0.6 - 2.1 cm long, 1.0 - 4.0 mm wide, the apices acuminate; heads 1 - numerous, borne singly on the peduncles; receptacle conical; involucre campanulate to hemispherical, 2.5 - 4.5 mm high, 0.5 - 1.2 cm wide; phyllaries imbricated in two equal series, ovate, lance-elliptic, or ovate-lanceolate to linear-lanceolate, 2.5 - 4.5 mm long, 0.8 - 1.8 mm wide, the margins scarious, prominently lacerate-ciliate above the middle, the green midportion glabrous or sparsely pubescent on the back, the apices ciliate-acuminate; ray florets 14 - 35, white, or lavender below and paler above especially toward the distal end, 0.65 - 1.2 cm long, 2.0 - 3.1 mm wide, the apex entire or 2- or 3-toothed; disk florets 120 - 170, the limb 1.5 - 2.3 mm long, abruptly contracted at the throat, the lobes 0.5 - 0.6 mm long; stylar appendages of the disk ovate, about as long to twice as long as the stigmatic lines; achenes obovate, sometimes narrowly so, 1.0 - 1.6 mm long, 0.6 - 0.8 mm wide, sparsely to densely and evenly glochidiate-pubescent, the apical hairs sometimes so dense as to simulate a pappus crown, rarely a few achenes glabrous and then mostly within the same capitulum, greenish-brown to dark-brown; pappus absent or a minute, whitish or yellowish crown less than 0.1 mm high; chromosome number $\underline{n} = 4$, determined from PMC squashes.

Distribution: from Nuevo Leon, Mexico, northward into east-central and eastern Texas, eastern Oklahoma, and southernmost Kansas,

east into Missouri and Arkansas where it hybridizes with subsp. integrifolium. This widespread taxon occupies a wide array of habitats, ranging from dry to moist open pastures, roadsides, and native prairie to oak-pine, oak-elm, oak-hickory, and oak-pine-hickory woodlands. Data from herbarium specimens indicate a wide range of soil types, from sandy soils to sandy-loam, sandy-clay, and clay soils. Principal flowering dates in April and May, with a few early collections obtained in March, and a few late ones in June and July. Plate 14.

Representative specimens:

ARKANSAS: CLEBURNE CO.: dry bluffs, Van Buren, elev 550 ft, 29 June 1937, Demaree 15309 (F; MO); dry rocky ridges, Tumbling Shoals, elev 450 ft, 19 May 1951, Demaree 30490 (SMU, 2 sheets). CRAWFORD CO.: Pine Springs, 8 May 1938, Moore 380016 (WIS). FAULKNER CO.: Cedar Park, near Conway, 17 May 1933, Haas s. n. (TENN). HOT SPRINGS CO.: rocky creek bottoms, Chamberlain Creek, Magnet Cove, elev 550 ft, 2 May 1937, Demaree 14822 (F; MO); Chamberlain Creek bottoms, Magnet Cove, elev 490 ft, 1 May 1938, Demaree 17254 (SMU); Chamberlain Creek bottoms, Magnet Cove, elev 450 ft, 30 April 1939, Demaree 19034 (MO; SMU; UC). HOWARD CO.: small rocky creek bottoms, Saline River, Dierks, elev 420 ft, 3 May 1955, Demaree 36556 (KANU; SMU). JOHNSON CO.: glade, 1 mi NW of Piney, 3 May 1940, Rubricht B 1781 (MO). MONTGOMERY CO.: rocky wooded creek bottom, Caddo Gap, 23 May 1954, Demaree 35306 (SMU, 2 sheets). POLK CO.: bottoms of Cossatot River, elev 1000 ft, 3 May 1955, Demaree 36609 (KANU; SMU). PULASKI CO.: Little Rock, 10 May 1885, Hasse s. n. (F). SALINE CO.: small creek bank, branch of Alum Fork, State Hospital, elev 260 ft, 28 May 1954,

Demaree 35338 (KANU; SMU, 2 sheets). SEBASTIAN CO.: S of Greenwood, 2 May 1951, Moore 510068 (SMU). SEARCY CO.: rocky creek bottoms, St. Joe, elev 700 ft, 21 June 1941, Demaree 22263 (MO; SMU). KANSAS: CHAUTAUQUA CO.: rocky soil, 7 May 1897, Hitchcock 1055 (GH; MO); small, overgrazed pasture in scrub-oak woodland, sandy soil, 3 mi E of Sedan, 2 May 1961, McGregor 16841 (KANU; MSC). OKLAHOMA: ADAIR CO.: along bank of Little Lee Creek, 15 mi SSE of Stillwell, 6 May 1950, Hutchinson 43 (OKL); in oak-hickory woods, hill near Brushy Mountains, 12 mi S of Stillwell, on US 59, 12 May 1958, Wallis 6812 (KANU; SMU; TEX). ATOKA CO.: 7 mi W of Atoka, clay soil, woods and ravine near Hwy, 19 May 1944, Hopkins, Nelson & Nelson 360 (OKL); sticky red sandy clay, roadside, 4 mi S of Kiowa, 28 April 1955, Shinners 19781 (SMU). CANADIAN CO.: wet woods and cliff, Devil's Canyon, 5 mi E of Hinton, 25 April 1937, Ball 1447 (OKL). CARTER CO.: loam soil, Murray Lake, 11 April 1939, Felts 28 (OKLA); clay washes near Ardmore, 17 April 1913, Stevens 77 (GH). CHEROKEE CO.: rocky sandy loam soil, McSpadden Falls, 7.8 mi NE of Tahlequah, 2 May 1947, Rhoades 94 (TEX); prairie area, 3 mi E of Ft. Gibson, on state 10 and 1 mi N, 26 April 1958, Wallis 6484-1 (KANU; SMU; TEX). CLEVELAND CO.: dry, clayish upland, 4 mi E of Norman, 24 April 1928, Barkley s. n. (OKL 12143); prairies, E of Lexington, 6 May 1931, Jeffs s. n. (OKL 12147). COAL CO.: dry, rocky hillside, Tupelo, 10 April 1936, Demaree 11975 (OKL); COMANCHE CO.: sandy loam soil, meadow, 13 mi E of Lawton, 1 mi S, 26 April 1941, Mease 41 (OKL); sandy loam soil, Medicine Park, 17 April 1937, Root 77 (OKLA); moist soil, Wichita Mountains, 7 May 1921, Stemen 207 (OKL). CHOCTAW CO.: sandy loam soil,

5 mi E of Hugo, 19 April 1940, Kramer 99 (SMU). CREEK CO.: Sapulpa, 19 June 1894, Bush 253 (GH; MO); gravelly clay hillside, 13.5 mi E of Drumright, 8 June 1928, Shannon 13 (OKLA); waste places, Bristow, 3 May 1940, Williams 39 (OKL). HASKELL CO.: meadow soil, 3 mi W of Keota, 29 April 1939, Clark & DeVitt 22 (OKL). HUGHES CO.: dry pasture along Hwy 12, 4.7 mi E of county line between Hughes and Pontotoc counties, 20 April 1961, De Jong 789 (MSC); dry roadside, 6 mi E of Holdenville, 7 May 1937, Hopkins 1623 (OKL). JEFFERSON CO.: Waurika Lake, near Waurika, 15 April 1957, Hornuff s. n. (OKL). JOHNSTON CO.: moist, unshaded creekbank near Mannsville, April 1916, Griffith 3455 (GH); open woods and rocky glade in Tishomingo granite formation, 6 mi S of Mill Creek, 29 May 1940, Hopkins 4930 (OKL); in woods and meadows, near Tishomingo, 27 April 1916, Houghton 3549 (GH). KAY CO.: Tonkawa, 11 May 1907, Stewart 98 (F); sandy clay soil, E of Clay Hills, Blackwell, 29 April 1945, Byler 324 (OKLA). LATIMER CO.: in rich meadow along Rock Island R. R. W of Hughes, 21 May 1944, Hopkins, Nelson, & Nelson 516 (OKL); sandy loam, Wilburton, 9 May 1937, Standish 20 (OKLA). LEFLORE CO.: Goat's Bluff, near Summerfield, along stream, 27 April 1936, Mason 94 (OKL, 2 sheets); upland prairies, sandy soil, near Howe, 25 May 1931, Palmer 39343 (GH; MO). LOVE CO.: sandy loam, Lake Murray park, 24 April 1937, Beard 81 (OKL). MAYES CO.: rocky soil in wood, near Camp Scott, Locust Grove, 3 May 1940, Traylor 77 (OKLA); prairie area, half a mile N and 1 mi W of Peggs on State 82, 11 May 1958, Wallis 6675 (KANU; SMU; TEX). MCCURTAIN CO.: oak-pine woods, Beavers Bend State Park, 6 mi N, 4 mi E of Broken Bow, 18 April 1959, Harms 191 (KANU); open woods, near Idabel, 18 May 1916, Houghton 3645 (GH); oak-hickory-pine forest along road between the

Narrows and Smithville, 8 June 1930, Little & Olmsted 141 (OKL). MCINTOSH CO.: prairies along railroad, Checotah Road, 2 May 1939, Bebb 4851 (OKL). MURRAY CO.: Arbuckle Mountains, Crusher, 12 May 1916, Emig 606 (MO); moist soil, banks of Washita, near Dougherty, 25 May 1907, Rutledge & Gage s. n.(OKL 12139); SE of Sulphur, 13 April 1926, Stemen 425 (OKL). MUSKOGEE CO.: prairie, roadside, moist black loam soil, 1 mi NE of Muskogee, 9 May 1926, Little 127 (OKL); sand-waste field, 3 mi E of Bragg, April 1950, Myers 62 (SMU); floodplain of Little Greenleaf Creek, E of Camp Gruber, 6 May 1950, Rohrbaugh 173 (OKL). NOBLE CO.: sandy clay soil, 2.5 mi E of Morrison, 1 May 1937, Perrin s. n. (OKL; OKLA 20162). OKLAHOMA CO.: moist soil, pasture, 3 mi E of Oklahoma City, 1 May 1924, Mosley 73 (OKL); sandy soil in open postoak-blackjack woods, 6 mi E of Britton, 17 May 1941, Waterfall 2702 (GH; OKL). OKMULGEE CO.: sandy clay loam, 8 mi E, 2 mi S of Mounds, 25 March 1937, Perrin 30 (OKLA). OSAGE CO.: clay loam soil, 6 mi NE of Prue, 24 April 1937, Cowley 10 (OKL); sandy soil, oak-hickory open wooded area, 8 mi N of Pawhuska, 3 May 1958, McGregor 13841 (KANU); Boy Scout Camp, 15 mi W of Bartlesville, 10 May 1941, Rice 141 (OKL). PAYNE CO.: low spot in pasture, 6 mi N of Stillwater, 15 June 1951, Coryell 995 (OKLA); loam soil, near Stillwater, 1 May 1935, Measman 17 (PH; TEX). PITTSBURG CO.: open woods, E of Hartshorne, 11 June 1930, Clark 2629 (OKL); dry pasture along Hwy 270, 6.5 mi E of Arpellar, 20 April 1961, De Jong 783 (MSC); rocky soil, open blackjack forest, Lake McAlester, 15 April 1941, Henson 224 (OKLA); black sandy loam, 3.4 mi N of Kiowa, 28 April 1955, Shinners 19791 (SMU). PONTOTOC CO.: loam soil, 4 mi S of Stonewall, 16 April 1938, Fry 125 (TEX); well-drained meadow in Wintersmith Park,

1 mi SE of Ada, 2 April 1951, McCoy 520 (OKLA); oak-hickory open woods, 5 mi S of Allen, 10 May 1952, McCoy 2701 (OKLA). POTTAWATOMIE CO.: woodland, 1 mi SW of Tecumseh, 28 June 1937, Barkley 1353 (MO; OKL); prairie, W of Pink, 3 April 1932, Ducker 47 (OKL). PUSHMATAHA CO.: roadside, 8 mi NE of Antlers, 16 April 1954, Brown s. n. (OKL); 1 mi S of Nashoba, 31 May 1949, Clark 363 (TEX); dry, rocky oak-elm woods, 3 mi W of Corinne, 15 April 1955, Hardin 559 (GH; MICH); dry, rocky barrens, 4 mi E of Albion, 9 May 1937, Hopkins & Cross 1788 (OKL); 4 mi NE of Finlay, 9 May 1937, Hopkins 1881 (OKL). SEMINOLE CO.: open fields and roadsides near Wewoka, 12 May 1940, Nelson 62 (OKL). SEQUOYAH CO.: open field and roadside at Dwight Mission, 6 mi NE of Sallisaw, 7 May 1955, Wallis 2073 (OKLA); oak woods at Tenkiller Lake, 5.5 mi NE of Gore, on state 100, 7 May 1957, Wallis 3816 (OKLA). ROGERS CO.: Catoosa, 8 May 1895, Bush 897 (MO). STEPHENS CO.: 3 mi SW of Marlow, 2 May 1941, Rice 38 (OKL). TULSA CO.: sandy loam roadside, S of Sand Springs, 30 April 1938, Baldock 313 (TEX); oak-hickory association, vicinity of Tulsa, 29 April 1937, Luckhardt 209 (OKL). WAGONER CO.: loam of prairie, Wagoner, 28 May 1920, Pennell 10603 (PH).

TEXAS: ANDERSON CO.: oak-pine woods on gentle slopes, Lake View Methodist Assembly Grounds, 12 April 1955, Hardin 527 (GH; MICH); near Palestine, 1 April 1935, Whitehouse 10262 (MICH; SMU). ARANSAS CO.: Aransas Refuge, 9 April 1945, Cory 48950 (GH; SMU). AUSTIN CO.: dry sandy soil, San Felipe de Austin State Park, 8 mi E of Sealey, 28 March 1949, Cory 55069 (SMU); Industry, 12 April 1936, Tharp s. n. (MO 1303939; TEX). BASTROP CO.: sandy roadside, 6 mi SE of Elgin, 18 April 1945, Shinners 7264 (MO; SMU); gravelly soil, 5 mi W of Bastrop, 18 April 1945, Shinners 7272 (SMU). BEE CO.: roadside

pasture, 4 mi SW of Skidmore, 28 March 1948, Cory 54127 (KANU; SMU). BRAZORIA CO.: sandy prairies, Columbia, 25 March 1914, Palmer 5028 (MO). BRAZOS CO.: woods, 14 mi SE of College Station, 21 April 1936, Anderson & Hubricht s. n. (MO 1105098); old sandy field, 2 mi SW of College Station, 20 April 1946, Cory 51568a (SMU); clay barrens, Bryan, 27 May 1915, Palmer 7785 (MO; TENN). CALDWELL CO.: Luling, 28 March 1930, Tharp 7331 (TEX). CALHOUN CO.: prairie, Magnolia Beach, 1 April 1934, Whitehouse 10421 (SMU). CHAMBERS CO.: without locality, 1936, Tharp s. n. (TEX). CHEROKEE CO.: Marissa, 7 April 1916, Palmer 9388 (MO). CLAY CO.: sandy prairie, near Henrietta, 16 April 1939, McCart 1931 (SMU). COLORADO CO.: sandy soil, open areas of oak woodland, 8 mi NW of Eagle Lake, 5 April 1958, Turner 4350 (TEX); near Eagle Lake, 20 April 1934, Whitehouse 10416 (SMU). COOKE CO.: sandy roadside, 10.8 mi E of Gainesville, 7 May 1950, Shinners 12408 (SMU). DENTON CO.: post oak woods, 4 mi E of Denton, 23 April 1940, McCart 1985 (SMU); sandy hillside, open oak woods, 3.5 mi SE of Denton, 30 April 1950, Shinners 12302 (SMU); post oak belt, E of Roanoke on Hwy 114, 2 mi W of Tarrant Co. line, 13 April 1946, Whitehouse 15203 (MICH; SMU; UC). DEWITT CO.: sandy soil, without locality, 27 March 1942, Riedel s. n. (TEX). ERATH CO.: Cemetary, Rocky Point Road (Stephensville?), 4 May 1955, Hoisington 257 (OKL). FANNIN CO.: sandy ditch bank, 4 mi N of Bonham, 10 June 1945, Shinners 7842 (SMU). FAYETTE CO.: La Grange, elev 250 ft, 22 April 1942, Fisher 42058 (F; TEX, 2 sheets); sandy loam, sparse mesquite-post oak woods, Hwy 95, 0.6 mi N of Cistern, 2 April 1955, Johnston & McCart 5151 (TEX). FORT BEND CO.: close mounds of sandy loam, Richmond, 20 April 1899, Bray 99 (TEX). FREESTONE CO.: open

field, loamy oak soil, NW of Fairfield, 29 March 1935, Wiegand & Wiegand 2393 (GH). GALVESTON CO.: Galveston Island, May 1894, Schneck s. n. (F). GOLIAD CO.: Victoria, 29 March 1930, Tharp 7332 (TEX). GONZALES CO.: sandy woods, Ottine, 7 March 1926, Bogusch 1712 (TEX); sandy soil, 10 mi SE of Waelder, 12 March 1955, Turner 3711 (OKLA; SMU; TEX). GRAYSON CO.: sandy loam, N side of Katy RR going to Bells, 20 April 1947, Gentry 176 (TEX); Denison, 13 April 1931, Knaut s. n. (TEX); Sherman, 1889, Nash s. n. (MSC 82459; WIS). GUADALUPE CO.: roadside park, in sandy post oak woodlands, Hwy 123, 11 mi S of Seguin, 24 March 1955, Johnston & McCart 5045 (SMU). HARRIS CO.: along railroads, near Houston, 23 April 1899, Eggert s. n. (MO 122893). HARRISON CO.: sandy roadside embankment, 4.5 mi NE of Marshall, 9 May 1945, Shinners 7572 (SMU). HENDERSON CO.: sandy post oak woods, ca 6 mi NW of Athens, 20 April 1940, Lundell & Lundell 8499 (MICH; SMU); silt loam, open ground, 15 mi E of Sulphur Springs, 3 May 1945, Shinners 7482 (GH; SMU; UC). HUNT CO.: sandy clay pasture, 2.2 mi NE of Greenville, 23 April 1950, Shinners 12242 (SMU). JACK CO.: sandy and rocky roadside, 4.1 mi NE of Jacksboro, 30 April 1950, Shinners 12351 (SMU). JEFFERSON CO.: without locality, 20 April 1930, Tharp 7328 (TEX). KAUFMAN CO.: sandy prairies, Terrell, 6 April 1903, Reverchon 4006 (MO, 2 sheets; SMU); red brown silty clay loam, 8 mi E of Terrell, 8 May 1945, Shinners 7552 (SMU); sandy clay roadside, 2.5 mi SE of Kemp, 10 April 1949, Shinners 10857 (SMU). KENEDY CO.: sand in wet area, near Norias, Kings Ranch, 15 March 1942, Lundell & Lundell 10736 (MICH; SMU; TEX). KERR CO.: without locality, 8 June 1929, Whitehouse s. n. (MICH; TEX). LAVACA CO.: sandy roadside, 11.5 mi N of Hallettsville, 29 March 1949, Shinners 9939 (SMU). LEE

CO.: sandy soil, openings in post oak woodlands, elev 450 ft, 2 mi W of Lexington, 14 April 1950, Gould 5507 (SMU; TEX; UC). LEON CO.: sandy soil on slope above creek, 3 mi W of Normangee, 27 March 1949, Cory 55052 (SMU); open sandy ground, 13 mi SW of Buffalo, 10 April 1945, Shinners 7131 (MO; OKLA; SMU; TEX). LIBERTY CO.: Cleveland - Dayton, 19 April 1930, Tharp 7330 (TEX). MATAGORDA CO.: Palacios, elev 25 ft, 2 March 1938, Fisher 38055 (SMU; TEX); Matagorda, 5 March 1914, Palmer 4855 (MO). MONTAGUE CO.: alluvial sands, post oak belt, 3 mi W of St. Jo, 31 March 1946, Whitehouse 15033 (SMU). NACOGDOCHES CO.: broad shallow borrow ditch of Hwy, ca 4 mi SE of Melrose, 20 April 1950, Cory 57300 (SMU). NUECES CO.: Corpus Christi, 15 May 1936, Parks 42-115 (GH). RAINS CO.: sandy clay between Hwy and railroad, 2.5 mi NW of Point, 22 April 1953, Shinners 14355 (SMU). REFUGIO CO.: sandy bank, 15.25 mi SW of Refugio, 28 March 1948, Shinners 9918 (SMU). SAN PATRICIO CO.: 6 mi NE of Sinton, in Welder Wildlife Refuge, 6 March 1959, Turner 4466 B (TEX, 2 sheets). TARRANT CO.: open fields, Ft. Worth, 8 May 1905, Bebb 2487 (OKL; WIS); woodland, between Grapevine and Roanoke (Denton Co.), 11 May 1955, Lundell & Lundell 13747 (SMU); open grounds at Handley, 15 April 1913, Ruth 74 (PH); sandy soil, 3 mi W of Arlington, 6 April 1950, Speir 14 (KANU). TAYLOR CO.: abandoned field, 18 mi SW of View on Edwards Plateau, 11 May 1943, Tolstead 7224 (GH; MICH; MO; SMU; TEX; UC). TITUS CO.: sandy clay roadside, 8 mi SE of Mt. Pleasant, 13 April 1958, Shinners 26885 (SMU). TRAVIS CO.: Austin, 4 April 1914, Young s. n. (TEX). VAN ZANDT CO.: sandy open ground, 2 mi E of Grand Saline, 4 May 1945, Shinners 7534 (SMU); bare soil among grasses in prairie, silt loam, 3 mi E of Wills Point, 4 May 1945, Shinners 7541 (SMU);

sandy clay slope in road cut, 12 mi W of Canton, 3 April 1949, Shinners 10818 (SMU); sandy pasture, 1 mi E of Martin's Mills, 7 May 1939, Timmons 539 (SMU). VICTORIA CO.: sandy prairies, Victoria, 5 March 1916, Palmer 9070 (MO). WALKER CO.: open woods, sandy soil, Riverside, 24 March 1918, Palmer 14162 (WIS). WALLER CO.: dry banks, Hempstead, 24 April 1872, Hall 306 (F, MO). WEBB CO.: Laredo, Feb & March 1913, Orcutt 5564 (MO). WHARTON CO.: sandy soil, road ditch bank - road shoulder, 2 mi S of El Campo, 25 March 1949, Trew 209 (TEX). WILSON CO.: sandy roadside, 4.25 mi N of Stockdale, 27 March 1948, Cory 54065 (KANU; SMU). WISE CO.: post oak woods, 2 mi NE of Park Springs, 21 April 1939, McCart 1624 (SMU). COUNTY UNKNOWN: "San Felipe de Austin", 1835 Drummond 221 (lectotype, NY , photo MSC!; isotypes, GH!; GL!; K ; NY!).

MEXICO: NUEVO LEON: near Monterrey, 20 March 1900, Canby 125 (GH); in valley near Villa Santiago, by irrigation ditch, Barkley & Johnson 16121 n (F; TEX); Obispado, elev 1600 ft, 1 March 1947, Lacas 228 (F); Hacienda Vista Hermosa, 35 mi S of Monterrey, elev 2500 ft, 26 June 1939, White 1527 (GH; MICH).

The type of Bellis ciliata Raf. was not indicated by Larsen (1933) in her monograph of Astranthium. Rafinesque (1837) based his species on specimens collected by Thomas Drummond in Texas and sent to him by John Torrey. Two of Drummond's specimens are in the Torrey collection at the New York Botanical Garden (fide Dr. Bassett Maguire) and one of these has been designated as a lectotype. The New York specimens bear the data "Texas. Drummond. Coll. II. No. 221!". Specimens of the same collection at the Kew Herbarium (K) bear the locality

name "San Felipe" and the date "1835" (fide Dr. John H. Beaman). This locality refers to "San Felipe de Austin" where Drummond stayed several times during his exploration of Texas (cf. McKelvey, 1955).

Larsen (1933) reduced Bellis ciliata Raf. to varietal status under Astranthium integrifolium, but it is here recognized as a subspecies. The recognition of subspecies rather than varieties is prompted by the considerable ranges of the typical subspecies and subsp. ciliatum, and the relatively narrow zone of overlap. The two subspecies are separated from one another by quantitative characters and may be recognized without difficulty throughout their respective ranges. The occasional failure of a single character is compensated for by other characters. The key differences between the two subspecies hold true when they are grown in the greenhouse under uniform conditions.

Considerable taxonomic difficulties are encountered in the zone of overlap where subsp. integrifolium and subsp. ciliatum hybridize. The number of specimens which combine characters of the two taxa is numerous, but not enough specimens are available from the zone of overlap to assess accurately the pattern of variation. Specimens from eastern Arkansas would be especially helpful in this respect. No conclusions other than the probability of hybridization between the two subspecies seem to be warranted until further field work is carried out in the area.

The meiotic irregularities in one morphologically intermediate population from Fayetteville, Arkansas, (De Jong 790) are discussed in the section on cytological studies.

6. Astranthium splendens De Jong, spec. nov.

Type: NUEVO LEON: in open pine-oak stand along gravel road to Dr. Arroyo, 18.1 mi S of Route 60, between KMs 28 and 29, elev 2480 m, 6 Sept 1961, De Jong 1244 (holotype, MSC!; isotypes, GH!; TEX!; UC!; US!)

Planta perennis, caudice brevi cum radicis fibrosis, caulibus simplicibus vel pauci-ramosis, ad 35.0 cm altis, erectis ascendentibus, vel decumbentibus, parce ad dense strigosis cum pilis patentibus; folia alterna, integra, folia basilaria persistentia vel decidua, spathulata vel oblanceolata, usque ad 8.0 cm longa et 1.0 cm lata, folia caulina inferiora spathulata ad anguste lanceolata, superiora gradatim minora, suprema parva, anguste lanceolata vel linearilanceolata, 1.0 - 3.0 cm longa, 1.0 - 4.0 mm lata; pedunculi ad 17.0 cm longa, vel nudi vel bracteam solitariam linearem minutam habentes; receptaculum nudum, alveolatum; capitula solitaria, terminalia; involucrum campanulatum, 4.0 - 6.0 mm altum, 0.8 - 1.6 cm latum, phyllariis 2-seriatis, oblanceolatis, lanceolatis, vel linearilanceolatis, 4.0 - 6.0 mm longis, 1.0 - 2.0 mm latis, scarioso-marginatis, marginibus lacerato-ciliatis; flores radii circa 20 - 35, 1-seriati, ligulis 0.9 - 1.5 cm longis, 2.0 - 2.7 mm latis, albis vel plano ventrali albis et plano dorsali pallido-lavendulis; flores disci circa 150 - 185, corollis 2.8 - 3.1 mm longis, flavis; achaenia radii et disci obovata vel oblanceolata, compressa, 1.7 - 2.1 mm longa, 0.8 - 1.1 mm lata, pubescentia cum pilis glochidiatis, sine pappo vel

cum corona papposa albida minus quam 0.1 mm longa; chromosomarum n = 9.

Perennial, to 35.0 cm high, from a vertical, fibrous-rooted caudex, this simple or branched, and if branched, forming multiple crowns; stems 1 - 10, decumbent or more commonly ascending or erect, simple or branched below the middle, greenish to reddish-purple, sparsely to densely strigose toward the base, less so toward the heads; peduncles to 17.0 cm long, naked or with a single, small, linear bract, densely white-pubescent below the heads; basal leaves spathulate or oblanceolate, to 8.0 cm long and 1.0 cm wide, the long-tapering bases ciliate, the lamina sparsely to densely pubescent above and below, the margins ciliate, the midrib sunken above and not always extending into the obtuse or mucronate apex; lower cauline leaves spathulate to oblanceolate, sparsely to densely pubescent above and below, the margins ciliate, the apices mucronate or acute; middle and upper cauline leaves reduced upward, similar to the lower cauline leaves in pubescence, the middle spathulate or more commonly narrowly oblanceolate, to linear-lanceolate, the margins ciliate, the apices acute or acuminate; upper leaves much reduced, the uppermost narrowly lanceolate to linear-lanceolate, 1.0 - 3.0 cm long, 1.0 - 4.0 mm wide, glabrous to moderately pubescent above, moderately to densely pubescent below, the margins ciliate, the apices acuminate; heads 1 - many, borne singly on the peduncles; receptacle conical; involucre campanulate, 4.0 - 6.0 mm high, 0.8 - 1.6 cm wide; phyllaries imbricated in two equal series, rarely in a single series, oblanceolate, lanceolate, or linear-lanceolate, 4.0 - 6.0 mm long, 1.0 - 2.0 mm

wide, the margins scarious and lacerate-ciliate above the middle, the green midportion of the outer phyllaries sparsely to densely pubescent on the back, that of the inner phyllaries glabrous to sparsely pubescent, the apices ciliate-acuminate; ray florets 20 - 35, white, or more commonly white above and lavender below, the lamina 0.9 - 1.5 cm long, 2.0 - 2.7 mm wide, the apex 2- or 3-denticulate; disk florets 150 - 185, the limb 2.8 - 3.1 mm long, abruptly contracted at the throat, the lobes ca. 0.7 - 0.9 mm long; stylar appendages of the disk ovate-lanceolate, about as long to one and a half times as long as the stigmatic lines; achenes obovate or oblanceolate, 1.7 - 2.1 mm long, 0.8 - 1.1 mm wide, greenish-brown to dark-brown, evenly glochidiate-pubescent; pappus absent or a small, whitish crown less than 0.1 mm high; chromosome number $\underline{n} = 9$, determined from PMC squashes.

Distribution: Nuevo Leon, in the Sierra Madre Oriental, south of Cerro Potosi and southward into Cerro Linadero, then eastward into Tamaulipas, at elevations between 2000 and 2500 meters. The species is found in moist oak forests, open pine-oak stands, and open grassy slopes and meadows. Principal flowering dates from June through September. Plate 16.

Specimens examined:

NUEVO LEON: moist, cool, open meadow along gravel road to Dr. Arroyo, 18.9 mi S of Route 60, between KMs 30 and 31, elev 2490 m, 6 Sept 1961, De Jong 1240 (GH; MSC; TEX; UC; US); in open pine-oak stand along gravel road to Dr. Arroyo, 18.1 mi S of Route 60, between KMs 28 and 29, elev 2480 m, 6 Sept 1961, De Jong 1244

(holotype, MSC!; isotypes, GH!; TEX!; UC!; US!); open grassy slopes, Sierra Madre Oriental, Cerro Linadero, Dulces Nombres, elev 2000 m, and just east of the border into Tamaulipas, 10 Aug 1948, Meyer & Rogers 2923 (MO); in fields and along waterways, Sierra Madre Oriental, around Alamar, ca 15 mi SW of Galeana, 5 June 1934, Mueller & Mueller 749 (GH; MICH; TEX); moist oak wood, Sierra Madre Oriental, Cieneguillas to Puerto Santa Ana, ca 15 mi SW of Galeana, 28 June 1934, Mueller & Mueller 897 (GH; MICH; TEX); Hacienda Pablillo, Galeana, 29 July 1936, Taylor 10 (MO; TEX).

Astranthium splendens and the following species, A. Beamanii, form a close alliance with A. robustum and A. integrifolium on the basis of the lavender rays which the four species have in common; all other species in the genus have white rays. The relationships between these species are correlated with their distribution. A. splendens and A. Beamanii are found in the Sierra Madre Oriental in the state of Nuevo Leon, A. robustum occupies montane habitats not far to the north in the Trans Pecos region of western Texas, and A. integrifolium extends from Nuevo Leon northward into the United States. The four species fall readily into two groups on the basis of life duration and root characters: A. splendens and A. Beamanii are perennials with fibrous-rooted caudices while A. robustum and A. integrifolium are tap-rooted and tap- or fibrous-rooted annuals respectively. In this alliance, A. splendens is most closely related to A. Beamanii and A. robustum is close to A. integrifolium.

A. splendens differs from A. Beamanii in the achenes, which are evenly glochidiate-pubescent in the former, and glabrous or rarely

with a few scattered glochidiate hairs in the latter. The rays of A. splendens never show the typical pattern of alternating bands of light and dark lavender found in the rays of A. Beamanii. The difference in chromosome number probably constitutes an effective barrier, and experimental hybrids of the two species showed 58.5 per cent pollen stainability. In addition, the two species are well separated geographically. A. Beamanii is found only on Cerro Potosi where it occupies alpine and subalpine elevations and extends downward to about 2700 meters elevation. On the other hand, A. splendens occupies somewhat drier habitats below 2500 meters elevation and its range is separated from that of A. Beamanii by a stretch of arid desert.

The chromosome number of A. splendens is $n = 9$. In the Astereae, $n = 9$ is a frequently occurring chromosome number and it is probable that $x = 9$ is the primitive basic number of the tribe (cf. Solbrig et al., 1964). However, if $x = 9$ were accepted as the primitive basic number in Astranthium from which the other base numbers were derived, it would require the postulate that A. splendens is more primitive than A. xylopodum which it is not. Although A. splendens is a perennial, it clearly occupies an advanced phyletic position on the basis of its small, ribless, glochidiate-pubescent achenes, fibrous-rooted caudex, and cauline leaves that are reduced upward. The presence of $n = 3$ in three species of the genus clearly indicates $x = 3$ to be a basic chromosome number. Consequently, A. splendens is best interpreted as a hexaploid on the base of $x = 3$.

7. Astranthium Beamanii De Jong, spec. nov.

Type: NUEVO LEON: Cerro Potosi, in alpine meadow on summit of mountain, elev ca 3650 m, 13 Sept 1960, De Jong 766 (Holotype, MSC!; isotypes, GH!; TEX!; UC!; US!).

Astranthio splendenti affinis, differt praecipue quod ligula florium radii plano ventrali alba et plano dorsali vel pallido-lavendula vel in alternis coloribus pallido-lavendula et violaceo-lavendula striata; achaenia glabra vel aliquando parce pubescentia cum pilis glochidiatis; chromosomarum n = 12.

Perennial, 3.0 - 35.0 cm high, from a short, horizontal, oblique, or vertical fibrous-rooted caudex, this simple or branched and then with multiple crowns especially in alpine plants, forming a dense mat of basal rosettes; stems 1 - few, rarely as many as 10, decumbent or more commonly ascending or erect, simple or sometimes branched below the middle, greenish to purple, densely strigose toward the base with coarse, spreading trichomes, sparsely to moderately strigose upward; peduncles 2.0 - 20.0 cm long, naked, or rarely with a single, minute, linear bract, the summits densely pubescent below the heads; basal leaves mostly persistent, rarely deciduous, spathulate, to 10.0 cm long and 1.0 cm wide, the tapering bases ciliate-pubescent, the lamina moderately pubescent above, often with sunken midrib and this not quite extending into the obtuse or mucronate apex, sparsely pubescent below especially on the prominent midrib, the margins ciliate or hardly so; cauline leaves reduced upward, the lower spathulate,

Plate 15. *Astranthium Beamanii*, drawn from *De Jong 769* (MSC).

narrowly oblanceolate, or linear-lanceolate, to 5.0 cm long and 8.0 mm wide, often much reduced, nearly glabrous to moderately pubescent above, moderately pubescent below especially on the midrib and toward the mucronate or acute apex, the margins ciliate; middle and upper cauline leaves narrowly lanceolate to linear-lanceolate, the uppermost often falcate, much reduced, 0.5 - 2.5 cm long, 0.9 - 3.0 mm wide, glabrous or with a few scattered hairs above, sparsely pubescent below, the margins ciliate, the apices acute or acuminate; heads large, borne singly on the peduncles; receptacle conical; involucre campanulate to hemispherical, 3.0 - 6.5 mm high, 0.8 - 1.5 cm wide; phyllaries imbricated in 2, rarely 3, equal series, 3.0 - 6.5 mm long, 1.0 - 2.0 mm wide, ovate to narrowly lanceolate, the scarious margins lacerate-ciliate above the middle and often reddish-purple, or, in alpine plants, the entire involucre reddish-purple and then the scarious margins less obvious, the green midportion sparsely to moderately pubescent on the back, the apices ciliate-acute or ciliate-acuminate; ray florets 15 - 30, the corolla 0.8 - 1.3 cm long, 2.5 - 4.0 mm wide, white above, pale to deep lavender below or with alternating bands of light and dark lavender, turning pale violet to deep blue-violet in drying, the apex 2- 3-dentate or 2 - 3-denticulate; disk florets 90 - 150, the limb 2.5 - 3.1 mm long, abruptly contracted at the throat, the lobes 0.8 - 1.0 mm long; stylar appendages of the disk ovate, somewhat shorter than to about as long as the stigmatic lines; achenes obovate or oblanceolate, glabrous or rarely with a few scattered glochidiate hairs, greenish-brown to dark-brown, 1.8 - 2.2 mm long, 0.9 - 1.1 mm wide; pappus absent or a minute whitish crown less than 0.1 mm high; chromosome number $n = 12$, determined from PMC squashes.

Plate 15.

Distribution: known only from Cerro Potosi in the Sierra Madre Oriental, state of Nuevo Leon, from the alpine meadow on the summit of the mountain (elevation ca. 3700 meters) down to an elevation of 2780 meters in Pinus Hartwegii forest. Principal flowering dates from June through September. Plate 16.

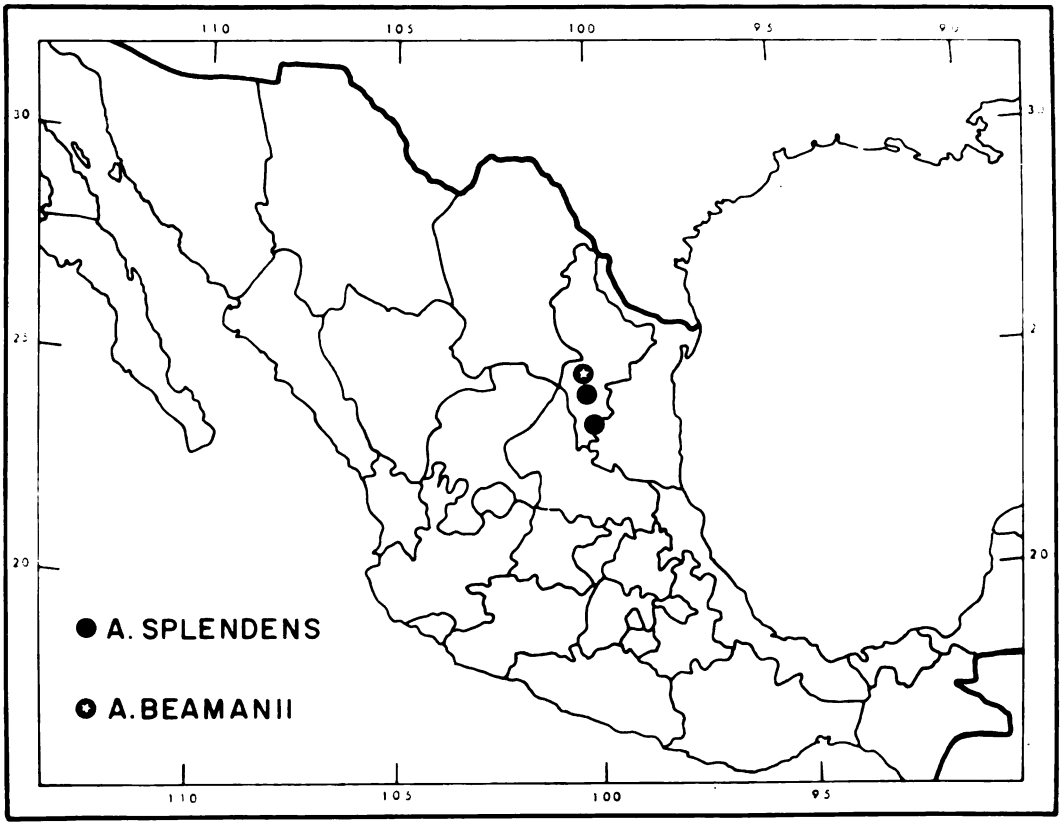
Specimens examined:

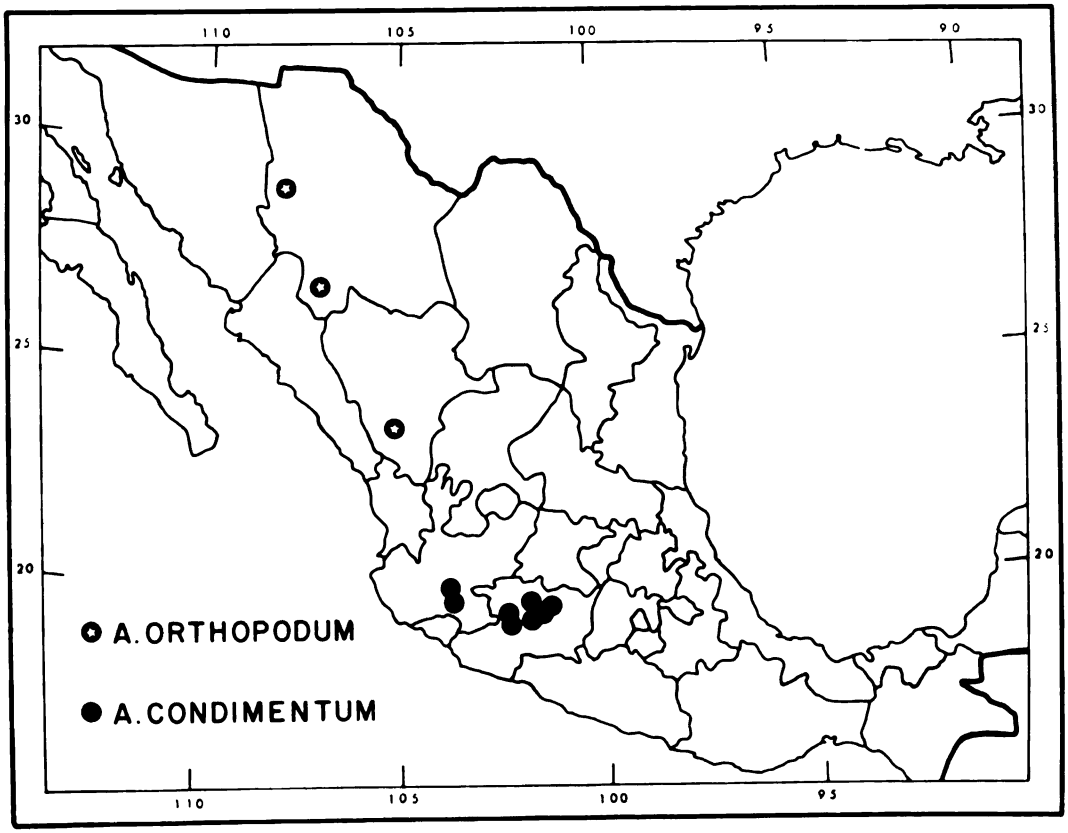
NUEVO LEON: in alpine meadow, top of Cerro Potosi, elev ca 3650 m, 1 July 1959, Beaman 2661 (MSC); Cerro Potosi, E side of mountain above Ejido 18 de Marzo, elev ca 2780 m, 25 June 1960, Beaman 3293 (MSC); gravelly soil at base of limestone cliff, SE slope of Cerro Potosi, elev ca 2900 m, 25 June 1960, De Jong 504 (GH; MSC); Cerro Potosi, on summit in alpine meadow, elev ca 3650 m, 26 June 1960, De Jong 509 (GH; MSC; TEX; UC; US); Cerro Potosi, near summit of mountain, on E side just below alpine meadow, elev ca 3600 m, 26 June 1960, De Jong 510 (GH; MSC; TEX; UC); Cerro Potosi, in alpine meadow on summit of mountain, elev ca 3650 m, 13 Sept 1960, De Jong 766 (holotype, MSC!; isotypes, GH!; TEX!; UC!; US!); Cerro Potosi, on E side of mountain in Pinus Hartwegii forest, elev ca 3260 m, 13 Sept 1960, De Jong 769 (GH; MSC; TEX; UC; US); in open rocky meadow, E side of Cerro Potosi, at KM 18 of road to telephone installation, elev 3375 m, 3 Aug 1962, Longpre 504 (MSC); Las Canoas on Cerro Potosi, Municipio de Galeana, 16 July 1935, Mueller 2172 (F; GH; MICH; MO; P; TEX); grassy openings in pine forest near peak of Cerro Potosi, elev 11,800 ft, 22 July 1938, Schneider 948 (GH; MICH; MO).

Since A. Beamanii is the only species of Astranthium which reaches alpine elevations, I take pleasure in naming this species in honor of Dr. John H. Beaman, student of the alpine and subalpine floras of Mexico and Guatemala.

The relationships of A. Beamanii with A. splendens were commented upon in the discussion of the latter. A. Beamanii is endemic to Cerro Potosi and has the narrowest distribution range of any species of Astranthium. Although its chromosome number, $n = 12$, could be interpreted both on a base of $x = 3$ and $x = 4$, its close relationship with A. splendens, which has $n = 9$ and is hexaploid on $x = 3$, suggests the species to be octoploid likewise on a base of $x = 3$.

Plate 16. Geographic distribution of *Astranthium splendens*, *A. Beamanii*, *A. orthopodum*, and *A. condimentum*.


110
105
100
95
30
25
20
● A. SPLENDENS
⊙ A. BEAMANII


110
105
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90
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25
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⊙ A. ORTHOPODUM
● A. CONDIMENTUM

8. Astranthium orthopodum (Robins. & Fern.) Larsen

Astranthium orthopodum (Robins. & Fern.) Larsen, Ann. Mo. Bot. Gard. 20: 31. 1933.

Bellis orthopoda Robins. & Fern., Proc. Am. Acad. 30: 117. 1894.

Type: CHIHUAHUA: Guachochic , 25 June 1892, Hartman 523 (holotype, GH).

Biennial or short-lived perennial, to 30.0 cm high, from a vertical, simple or somewhat branched, tap- or fibrous-rooted caudex, the stemroot junction prominently thickened or hardly so; stems 1 - many, simple or branched, erect, ascending, or sometimes decumbent, greenish to purple, sparsely to moderately strigose with delicate, rarely coarse, appressed to spreading trichomes; peduncles to 12.0 cm long, naked or with a single, minute, linear bract, moderately to densely pubescent below the heads; basal leaves narrowly spathulate to narrowly oblanceolate, with long-attenuate bases, the lamina sparsely to densely pubescent above and below, the margins ciliate, the apices obtuse or mucronate; lower cauline leaves narrowly spathulate to narrowly oblanceolate, to 3.0 cm long and 6.0 mm wide, but more commonly shorter and narrower, sparsely to densely pubescent above and below, the margins ciliate, the apices obtuse or mucronate; middle cauline leaves narrowly oblanceolate to linear-lanceolate, near-glabrous to sparsely pubescent above, moderately to densely pubescent below, especially on the prominent midrib, the margins often conspicuously ciliate, the apices cuspidate or acuminate; upper leaves much reduced and narrower, the

Plate 17. *Astranthium orthopodum*, drawn from *De Jong 984* (MSC).

uppermost linear-lanceolate to linear, 0.7 - 1.7 cm long, 0.8 - 2.1 mm wide, glabrous to sparsely pubescent above and below, with ciliate margins and long-acuminate apices; heads 1- numerous, borne singly on the peduncles; receptacle conical; involucre campanulate to hemispherical, 4.0 - 6.1 mm high, 0.9 - 1.4 cm wide; phyllaries imbricated in two equal series, ovate-lanceolate to linear-lanceolate, 4.0 - 6.1 mm long, 1.0 - 1.8 mm wide, the margins scarious, often purple, lacerate-ciliate above the middle, the green midportion sparsely to moderately pubescent on the back, the apices ciliate-acute or ciliate-acuminate; inner series similar to the outer but with more prominent scarious margins; ray florets 20 - 30, white, the corolla 1.1 - 1.6 cm long, 2.0 - 3.5 mm wide, the apices 2- or 3-toothed; disk florets 170 - 200, the limb 2.5 - 3.0 mm long, abruptly contracted at the throat, the lobes 0.7 - 0.8 mm long; stylar appendages of the disk ovate-lanceolate, slightly shorter than to about as long as the stigmatic lines; achenes obovate, rarely oblanceolate, compressed or hardly so, 1.2 - 1.8 mm long, 0.7 - 1.0 mm wide, light to dark brown, moderately and evenly glochidiate-pubescent; pappus absent or a conspicuous, but minute, whitish or yellowish crown less than 0.1 mm high; chromosome number n - 3, determined from PMC squashes. Plate 17.

Distribution: in the Sierra Madre Occidental in the states of Chihuahua and Durango, in open cool, meadows and open pine forests, at elevations between 2200 and 2400 meters. Principal flowering dates from May through August. Plate 16.

Specimens examined:

CHIHUAHUA: Guachochic , 25 June 1892, Hartman 523 (holotype,

GH!); vicinity of Madera, elev about 2250 m, 27 May to 3 June 1908, Palmer 287 (MO); prairie near San Juanito, Depto. de Bocoyna, elev 8000 ft, 26 July 1937, Shreve 8034 (GH). DURANGO: damp, grassy depression along Route 40, at edge of Pine-Madroño forest, 38 mi SW of Ciudad Durango, elev 2390 m, 8 Aug 1961, De Jong 984 (GH; MSC; TEX; UC; US); fields along Route 40, ca 31 mi SW of Ciudad Durango, 16 Aug 1960, King 3744 (MICH; MSC; TEX; UC); city of Durango and vicinity, April - November 1896, Palmer 163 (GH; MO; UC); Otinapa, 25 July - 5 Aug 1906, Palmer 425 (MO; UC).

Although Larsen (1933) indicated A. orthopodum to be perennial, greenhouse cultures of the species clearly showed it to be a biennial or short-lived perennial.

Astranthium orthopodum is a distinct species on the basis of its narrow leaves, erect or ascending stems, and often conspicuously swollen stem-root junction. Extending southward from the state of Chihuahua, the species reaches its southernmost limit in central Durango where it occurs abundantly in open meadows and pine forests along Route 40 between Ciudad Durango and Mazatlan.

The closest relative of A. orthopodum is A. condimentum whose range is not far to the south. In addition to resembling each other in morphological characters, the species both have $n = 3$ and their karyotypes are very similar. Experimental hybrids between the two species rarely showed meiotic irregularities, but the pollen grains of the hybrids showed only 54.0 per cent stainability. Astranthium condimentum is set apart from A. orthopodum by its wider leaves, decumbent stems, and the annual habit.

Astranthium orthopodum is also related to *A. robustum* whose range in the Trans-Pecos region of Texas borders on the state of Chihuahua. The two species resemble each other in the narrow leaves, the chromosome number of $n = 3$, and in karyotype characters.

9. Astranthium condimentum De Jong, nom. nov.

Chrysanthemum mexicanum HBK., Nov. Gen. et Spec. Pl. 4: 299. 1820.

Type: MICHOACAN: "Pazcuaro (Mexique)", without date, Humboldt & Bonpland 4347 (holotype, P ; photo MSC!; isotype, P!).

Annual, to 50.0 cm high, from a slender taproot with fibrous lateral roots; stems 1 - many, simple or much-branched, ascending, spreading, or more commonly decumbent, greenish to purple, sparsely to moderately strigose with often somewhat tangled hairs; peduncles to 15.0 cm long, naked or with a small, linear bract, moderately to densely pubescent below the heads; basal leaves spathulate, sparsely pubescent above and below, soon wanting; lower cauline leaves spathulate or oblanceolate to lanceolate, sometimes subulate, sparsely to moderately pubescent above and below, especially on the midrib, the margins ciliate or hardly so, the apices obtuse or mucronate; middle and upper cauline leaves gradually reduced in size and narrower, the uppermost narrowly lanceolate, subulate, or near-linear, 0.6 - 2.3 cm long, 0.8 - 3.5 mm wide, glabrous or sparsely pubescent above and on the midrib below, with ciliate margins and long-acuminate apices often tipped by a firm, whitish mucro; heads 1 - numerous (-40), borne singly on the peduncles; receptacle conical; involucre campanulate, 3.0 - 6.0 mm high, 0.7 - 1.3 cm wide; phyllaries in 2, rarely 1 or 3, equal series, the outer narrowly ovate or obovate to linear-lanceolate, 3.0 - 6.0 mm long, 0.7 - 2.0 mm wide, glabrous or with a few scattered

Plate 18. Astranthium condimentum, drawn from De Jong 1082 (MSC).

hairs on the green midportion, the margins scarious, often purple, lacerate-ciliate above the middle, the apices ciliate-acute or ciliate and long-acuminate; inner phyllaries similar, 1.0 - 2.0 mm wide; ray florets 15 - 35, white, sometimes roseate when dried, the corolla 1.0 - 1.4 cm long, 2.1 - 3.0 mm wide, the apex 2- or 3-toothed; disk florets 120 - 260, the limb 2.5 - 3.0 mm long, abruptly contracted at the throat, the lobes 0.5 - 1.0 mm long; stylar appendages of the disk ovate-lanceolate, about as long to about one and a half times as long as the stigmatic lines; achenes obovate, rarely oblanceolate, 1.3 - 1.8 mm long, 0.5 - 1.0 mm wide, glochidiate-pubescent, light to dark brown; pappus absent or a minute whitish crown less than 0.1 mm high; chromosome number $n = 3$, determined from PMC squashes. Plate 18.

Distribution: in the Sierra Madre Occidental, in Jalisco and Michoacan, and in the Transvolcanic Belt in Michoacan, south to Uruapan and east to Morelia, at elevations between 1900 and 2400 meters. The species is found in open pine forests, pastures, and along roadsides, in red clay-, silty clay-, and loam soils. Principal flowering dates from June through November, with a single collection obtained in January. Plate 16.

Specimens examined:

JALISCO: grassy roadside and open pine forest, along Route 110, 35 mi SW of Jiquilpan, elev 1980 m, 11 Aug 1961, De Jong 1027 (GH; MSC; TEX; UC; US); heavy red clay loam, grassy meadow near summit, Sierra del Tigre, 3 mi S of Mazamitla, elev 2100 - 2200 m, 10 Nov 1959, McVaugh & Koelz 425 (MICH); rocky soil, pine forest, 1 - 2 mi E of Tapalpa, elev 2100 - 2200 m, 30 Oct 1960, McVaugh 20496 (MICH).

MICHOACAN: open pine forest in volcanic ash soil, at KM 216 on Uruapan-Los Reyes road, 2 Sept 1958, Beaman 2417 (MSC); open pine stand, among grass, at KM 43.5 of Route 39 from Carapan to Uruapan, elev 2390 m, 7 Sept 1960, De Jong 760 (GH; MSC; TEX; UC; US); grassy roadside, between KMs 50 and 51, Route 39 from Carapan to Uruapan, 14 Aug 1961, De Jong 1080 (GH; MSC; TEX); open pasture, Route 160, 4 mi S of Villa Escalante, between Quiroga and Ario de Rosales, elev 2270 m, 15 Aug 1961, De Jong 1082 (GH; MSC; TEX); open roadside, 5.4 mi E of Quiroga, elev 2300 m, 17 Aug 1961, De Jong 1091 (GH; MSC; TEX; UC; US); "Pazquaro (Mexique)", without date, Humboldt & Bompland 4347 (holotype, P ; photo MSC!; isotype, P!) loamy soil, fields along Route 15, ca 33 mi W of Morelia, 5 Aug 1960, King 3631 (MICH; MSC; TEX; UC); low damp woods, Quinta Huitado, NW outskirts of Uruapan, 11 Jan 1941, Langman 3239 (PH); open pasture, 1 mi S of Tancitaro, elev 6200 ft, 27 July 1940, Leavenworth 375 (GH; MICH; MO); on road from Tancitaro to Apatzingan, elev 5000 ft, 17 Aug 1940, Leavenworth 649 (F); silty clay soil, pine forest, 3.5 mi N of Paricutin volcano, 14 June 1950, Turner 1885 (SMU); silty clay soil, National Park, Uruapan, 16 June 1950, Turner 1909 (MICH; SMU).

The transfer of Chrysanthemum mexicanum HBK to Astranthium requires a name change because the specific epithet has already been used in another combination in the genus (Astranthium mexicanum (A. Gray) Larsen). In the region around Paricutin volcano in Michoacan, the Tarascan Indians call this species "Concepcion", and Mr. Jose Cruz Gomez of the village of Anguahan assured me in 1961 that plants of this species are used as a flavoring agent for soups

and meats. I failed to locate plants of the species at local markets, however, and thus was unable to confirm its reputed qualities, until, a few days later, I came across a cultivated patch of "Concepcion" near the town of Quiroga. As a double check, however, since the species may be easily confused with Aphanostephus ramosus with which it is often found, I wrote Mr. Gomez two years later, requesting specimens of the "soup- and meat-flavoring plants". The specimens which he sent me were indeed Astranthium condimentum. It is in allusion to the reputed culinary qualities of the species, therefore, that I have coined the new epithet.

Astranthium condimentum is widespread in Michoacan where it is often found along roadsides and in pastures and then becomes somewhat weedy. It has been confused with species of Aphanostephus, especially A. ramosus and the two species may often be seen growing together. The latter is readily set apart at first glance by the reflexed rays and often toothed leaves. When plants of A. condimentum grow on bare soil, the branches are strongly decumbent and hug the soil. When plants grow in tall grass, however, the branches are erect or ascending.

As pointed out under A. orthopodum, the closest relationships of A. condimentum are with that species. This shows strongly in the karyotypes of the two species. A. condimentum also shows resemblance to A. integrifolium with which it shares genetic material as discussed in the section on crossing relationships in the genus, as well as to A. robustum on the basis of chromosome number and karyotype characters.

10. Astranthium robustum (Shinners) De Jong, comb. et stat. nov.

A. integrifolium (Michx.) Nutt. var. robustum Shinners, Field and Lab. 18: 158. 1950.

Type: TEXAS, Reeves County: infrequent along Hwy, limestone soil, 2 mi S of Toyahville, foothills of the Barilla Mountains, alt 3350 ft, 20 April 1947, Warnock 5126 (holotype, SMU!; isotype, SRSC!).

Robust annual, to 40.0 cm high, from a slender to stout, simple or somewhat branched taproot mostly without fibrous lateral rootlets; stems 1 - numerous, often decumbent, or ascending, simple or much-branched above and below the middle, greenish to reddish-purple, sparsely to densely strigose with coarse trichomes; peduncles to 15.0 cm long, naked or with a single minute, linear bract, moderately to densely pubescent below the heads; basal leaves narrowly to broadly spathulate, 1.0 - 8.0 cm long, 0.3 - 1.6 cm wide, the lamina sparsely to densely strigose above, the lower surface nearly glabrous throughout or only strigose on the midrib, the margins sparsely to moderately ciliate, the apices obtuse or mucronate; cauline leaves similar to the basal leaves in characters of pubescence, often densely crowded on the stems, the midrib prominent toward the base, the margins ciliate, the apices provided with a prominent, white mucro; lower cauline leaves often withering, spathulate to narrowly oblanceolate, 0.9 - 1.4 cm long, 0.3 - 1.1 cm wide, the apices mucronate; middle cauline leaves reduced upward, narrowly spathulate to narrowly lanceolate; uppermost

leaves much reduced, narrowly spathulate to linear-lanceolate, 0.7 - 1.8 cm long, 1.0 - 2.8 mm wide, the apices short- to long-acuminate; heads few to numerous (Cory 52255, SMU, has more than 100 heads), borne singly on the peduncles; receptacle conical; involucre campanulate to hemispherical, 4.0 - 6.8 mm high, 1.0 - 1.4 cm wide; phyllaries imbricated in 2, rarely 3, equal series, 4.0 - 6.8 mm long, 1.0 - 1.7 mm wide, lanceolate or narrowly so, sparsely to densely strigose on the back, the margins scarious and conspicuously lacerate-ciliate, the apices ciliate-acuminate; ray florets 18 - 35, white, or lavender below throughout or only on the distal half, often pinkish when dried, the lamina 0.9 - 1.3 cm long, 2.0 - 3.1 mm wide, the apex entire or minutely to prominently 2- or 3-toothed; disk florets 180 - 200, the limb 2.5 - 3.0 mm long, abruptly contracted at the throat, the lobes 0.7 - 0.8 mm long; stylar appendages of the disk ovate, about equal in length to three quarters the length of the stigmatic lines; achenes obovate to oblanceolate, 1.4 - 2.1 mm long, 0.7 - 1.2 mm wide, greenish-brown to dark brown, sparsely to moderately glochidiate-pubescent; pappus absent or a minute, whitish crown less than 0.1 mm high; chromosome number $n = 3$, determined from PMC squashes.

Distribution: known only from the Trans Pecos region of extreme SW Texas, north of Big Bend National Park, along arid roadsides, and in arid pine flats, low mesas, and mountain canyons. Frequently of weedy occurrence in orchards, golf courses, and school grounds. Found mostly at elevations between 800 and 1400 meters. Principal flowering dates from March through June. Plate 14.

Specimens examined:

TEXAS: BREWSTER CO.: apple orchard, 14 mi NW of Alpine, 12 April 1936, Cory 18541 (GH); low mesa, Alpine, 14 March 1926, Cottle W7-61 (SRSC); between Pecos and Alpine, 31 March 1942, Nelson & Nelson 5011 (GH; SRSC; UC); along Hwy, N of Alpine, 26 April 1936, Sperry T374 (SRSC); sand along Calamity Creek, 24 mi S of Alpine, elev 4500 ft, 2 April 1949, Turner 455 (SRSC); golf course, Alpine, 12 March 1937, Warnock T113 (GH; SRSC, 2 sheets); golf course, Alpine, 14 April 1938, Warnock T375 (TEX); campus, Sul Ross State College, Alpine, 6 June 1940, Warnock 20914 (TEX); Alpine, 7 June 1940, Warnock 20916 (TEX); pine hill flats, Glass Mountains, 2 June 1941, Warnock 21251 (TEX); red igneous soil, golf course, Alpine, elev 4600 ft, 24 May 1947, Warnock 5657 (SRSC); along stream at Leoncita Springs, Kokernot Ranch, elev 4000 ft, 30 April 1948, Warnock 7722 (MSC; SMU; SRSC, 2 sheets); igneous soil along Hwy, 18 mi S of Alpine, elev 4450 ft, 11 May 1951, Warnock 9956 (SRSC). JEFF DAVIS CO.: shoulder of Hwy, 7.4 mi S of Toyahville, 5 May 1946, Cory 52019 (SMU); roadside, 3.3 mi SE of Ft. Davis, 16 May 1946, Cory 53097 (SMU; UC); Ft. Davis, 1885, Girard s. n. (GH); igneous soil, Limpia Canyon, Davis Mountains, 28 mi N of Ft. Davis, elev 3700 ft, 20 April 1947, Warnock 5110 (SRSC, 2 sheets); sandy soil, along Hwy, 9 mi W of Valentine, elev 4500 ft, 2 May 1947, Warnock 5327 (SRSC); among igneous boulders, Limpia Canyon, 10 mi N of Ft. Davis, elev 4750 ft, 23 April 1949, Warnock 8449 (SMU; SRSC); Valentine, 20 April 1932, Whitehouse 8462 (TEX, 2 sheets). JEFF DAVIS-PRESIDIO CO.: Valentine-Marfa, 15 April 1949, Tharp & Havard 49413 (TEX). PECOS CO.: roadside, 20 mi SW of Ft. Stockton, 19 May 1946, Cory 53211 (SMU; UC). PRESIDIO CO.: 1 mi SE of Marfa, 3 April 1944,

Cory 44058 (GH; TEX); without locality, 11 May 1932, Garner 23 (TEX); Marfa, June 1936, Hinckley s. n. (TEX); ditch bank by school ground, Marfa, elev ca 4800 ft, March 1937, Hinckley 956 (SMU); ditch bank, Marfa, 8 May 1944, Hinckley 2942 (SRSC); Marfa, 1 April 1931, Knight s. n. (TEX); open ground along railway grade, near Marfa, 18 June 1926, Palmer 31036 (MO; PH); limestone, Pinto Canyon, E side of Chinati Mountains, elev 3200 ft, 26 April 1952, Scuddy 19 (SRSC); red sandy soil, 20 mi W of Marfa, elev 4600 ft, 2 May 1947, Warnock 5296 (SMU; SRSC); red sandy soil, 20 mi W of Marfa, elev 4300 ft, 18 May 1947, Warnock 5610 (SRSC, 2 sheets). REEVES CO.: roadside ditch, 7 mi SE of Davis Mountains Service Station, 9 May 1946, Cory 52248 (SMU; UC); 5 mi SE of Davis Mountains Service Station, 9 May 1946, Cory 52255 (SMU); infrequent along Hwy, limestone soil, 2 mi S of Toyahville, foothills of the Barilla Mountains, alt 3350 ft, 20 April 1947, Warnock 5126 (holotype, SMU!; isotype, SRSC!); sandy rocky soil, 20 mi N of Saragosa, elev 2900 ft, 15 May 1949, Warnock 8607 (SRSC). WITHOUT LOCALITY: Valley of the Pecos, 1951 - 1852, Wright 1175 (PH, 2 sheets); Pecos & Limpio, June 1851 - 1852, Wright 1176 (MO).

Although Shinners (1950) treated A. robustum as a variety of A. integrifolium, I consider it to be worthy of specific recognition. A. robustum differs from A. integrifolium subsp. integrifolium and A. integrifolium subsp. ciliatum in its more robust size, mostly decumbent stems with coarse rather than fine trichomes, crowded cauline leaves of thicker texture, more diffuse branching habit, more numerous heads, and the chromosome number of $n = 3$, rather than $n = 4$. Both A. robustum and A. integrifolium subsp. ciliatum occur in Texas, but

their ranges are well separated from one another. In addition, their habitat requirements are strikingly dissimilar. Subspecies ciliatum is found in areas of 30 - 50 inches of annual rainfall, on acid, sandy, or sandy-loam soils. On the other hand, A. robustum occurs in an arid desert region with less than 12 inches of annual rainfall, on calcareous soils, and often in arid montane habitats. On the basis of morphological, cytological, geographical, and ecological considerations, therefore, A. integrifolium var. robustum is here elevated to specific rank.

Astranthium robustum is considered to be the most advanced species of Astranthium on the basis of its annual habit and xerophytic adaptations. It is related to A. integrifolium and the rays are similar in color to those of A. splendens and A. Beamanii. The species also shows resemblance to A. condimentum and A. orthopodum and has the same chromosome number and karyotype as these two species.

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