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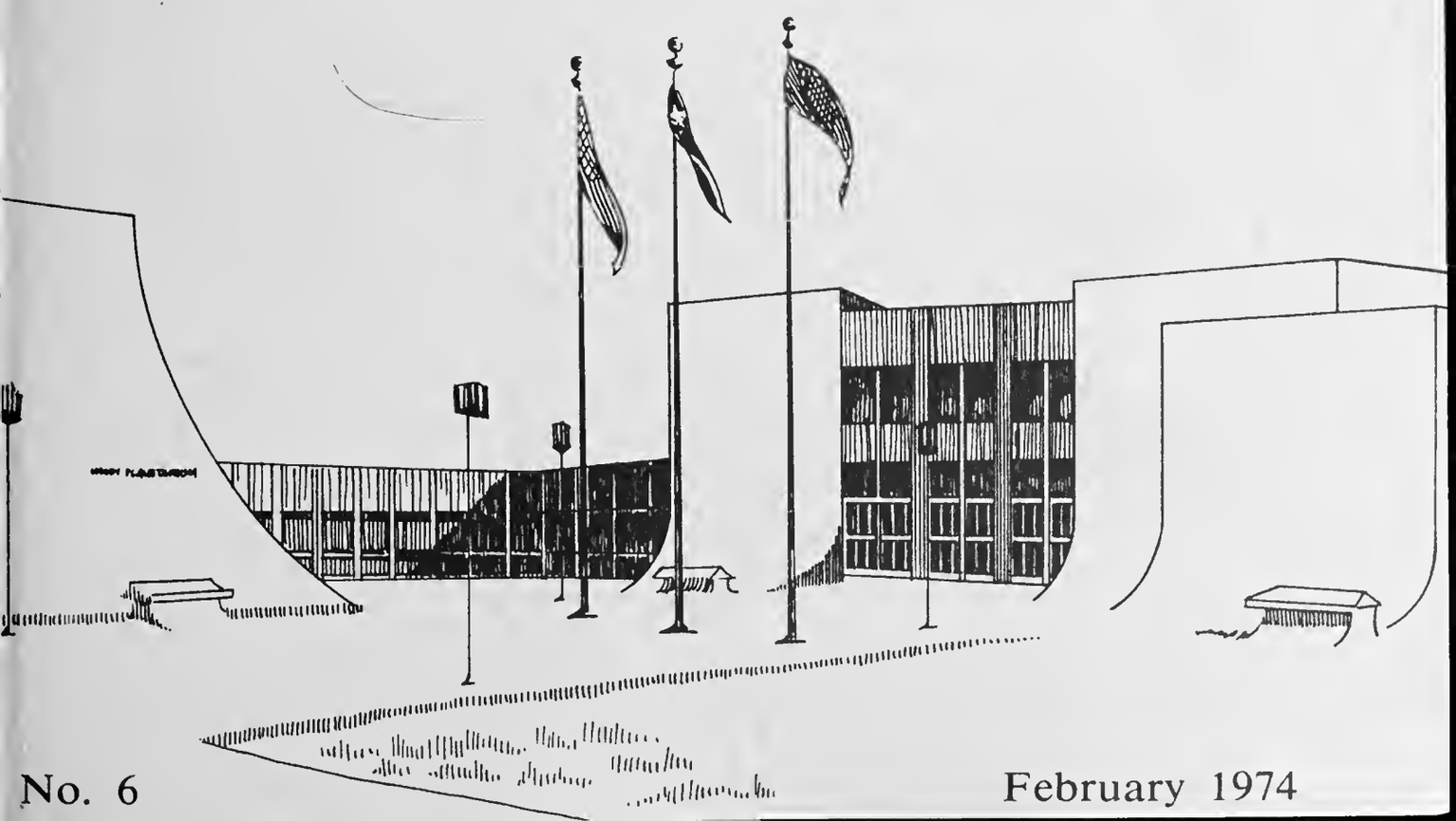
Systematic Studies of the Genus Pyrrhopappus (Compositae, Cichorieae)

David K. Northington



No. 6

February 1974

TEXAS TECH UNIVERSITY

The Museum
Special Publication No. 6
38 pp., 14 figs.
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David K. Northington

Pyrrhopappus is a well-defined genus of weedy herbs that frequently occurs in disturbed areas such as roadside ditches, lawns, and vacant lots of the southeastern and southwestern United States and adjacent Mexico. Because of their weedy nature and superficial resemblance to members of the common dandelion genus, *Taraxacum*, the plants of *Pyrrhopappus* are sometimes referred to as "false dandelions." They exhibit considerable plasticity of morphological characters, especially within the annual taxa. Most flower in spring or early summer and are readily distinguished from *Taraxacum* and related genera by their usually leafy stems, large, lemon-yellow flowers, and by the tendency of the heads to close at midday.

The number of species recognized in the genus has varied with the worker treating the group. For example, the late L. H. Shinners (1951, 1953) recognized five species for the state of Texas, whereas Correll and Johnston (1970) recognized only three. Such differing treatments undoubtedly reflect, at least to some extent, the plasticity of morphological characters mentioned above, with at least some of this due to natural hybridization and introgression between species. Shinners (1958) stated that introgression regularly occurs in north Texas between two of the annual taxa, *Pyrrhopappus carolinianus* and *P. multicaulis* var. *geiseri*. The conditions leading to hybridization are thought to be the establishment of disturbed habitats formed when different soil types are mixed in the building of highways, and the introduction of seed into these new habitats. The resulting roadside populations often contain a wide range of intermediates or character recombinations as well as the parental character combinations. Such populations, especially when represented by individuals on herbarium sheets, are difficult to evaluate taxonomically.

The genus was examined initially using palynologic and cytogenetic criteria, whereas the latter stages of the study emphasized chemosystematic approaches, especially at the populational level. The latter proved somewhat more useful in that specific chemical markers were found that correlated with certain morphological trends in the populations examined. Based on the cumulative information obtained by these various approaches, I here recognize six taxa (five species, one of which is divided into two varieties): *Pyrrhopappus carolinianus* (Walt.) DC., *Pyrrhopappus georgianus* Shinners, *Pyrrhopappus multicaulis* DC. var. *multicaulis*, *Pyrrhopappus multicaulis* DC. var. *geiseri* (Shinners) Northington (see Northington, 1973), *Pyrrhopappus rothrockii* A. Gray, and *Pyrrhopappus grandiflorus* (Nutt.) Nutt.

Taxonomic History

Pyrrhopappus was established in 1838 by De Candolle to accommodate *P. carolinianus* and several related taxa. *P. carolinianus* had at one time or another been placed in five different genera. Thus, Walter (1788) included this species in the Old World genus, *Leontodon*; Michaux (1803) placed it in *Scorzonera*; Pursh (1814) in *Chondrilla*, and Nuttall (1818) in *Borkhausia*. Finally, Rafinesque (1836) erected the genus, *Sitilias*, to accommodate the species. Although the last has priority, *Pyrrhopappus* held wide acceptance by subsequent workers and led to its conservation (Lanjouw *et al.*, 1966).

In addition to *Pyrrhopappus carolinianus*, De Candolle recognized five other species within the genus. These were divided into two sections: 1) Crinissa (from the Section Crinissa, genus *Chondrilla*), containing *P. carolinianus*, *P. multicaulis*, *P. scaposus*, *P. sessaeanus*, and *P. pauciflorus* and 2) Piesis, with a single South African species. Subsequent work has shown the South African member to be referable to *Taraxacum*. Of the remainder, only *P. carolinianus* and *P. multicaulis* are now recognized.

Gray (1876) extended the known range of the genus considerably westward when he described *Pyrrhopappus rothrockii*, a species of partially rhizomatous plants. This species occurs in Mexico, westernmost Texas, New Mexico, and southern Arizona. Unfortunately, Gray included elements of *P. rothrockii* in *P multicaulis*, thus inaccurately expanding the latter taxon's range. Shinners (1951, 1953) described two additional species, *P. geiseri* and *P. georgianus*, the latter being reduced to a variety of *P. carolinianus* by Ahles (1964). Probably the best treatment of *Pyrrhopappus* has been that of Gray (1888). With relatively minor exceptions, his taxonomic treatment of the genus is similar to my own. I recognize only two addititional taxa (one species and one variety).

Pollen Studies

Several workers have used pollen morphology, particularly at the generic level, in their taxonomic investigations of the tribe Cichorieae (Babcock, 1947; Davis and Raven, 1962). In the most recent comprehensive treatment of the Cichorieae, Stebbins (1953) used pollen characters to a considerable extent in his alignment of genera into tribes. According to Stebbins, most of the Old World genera and many of the New World genera of the Cichorieae have pollen of the type characterized by Wodehouse (1935) as echinolophate (ridges bearing spines) with three apertures. A number of genera, mostly New World, are characterized by a less elaborate sculpturing, termed echinate.

In this study, the external pollen morphology and the size ranges of the pollen within the genus *Pyrrhopappus* have been determined. Four of the diploid ($n=6$) and the single tetraploid ($n=12$) species (see section on chromosomal studies) were selected to determine the usefulness of pollen data for identification at the species level.

Materials and methods.—Heads with buds just prior to anthesis were selected from dried specimens collected in the field by me or from herbarium specimens at The University of Texas or from Southern Methodist University. These buds

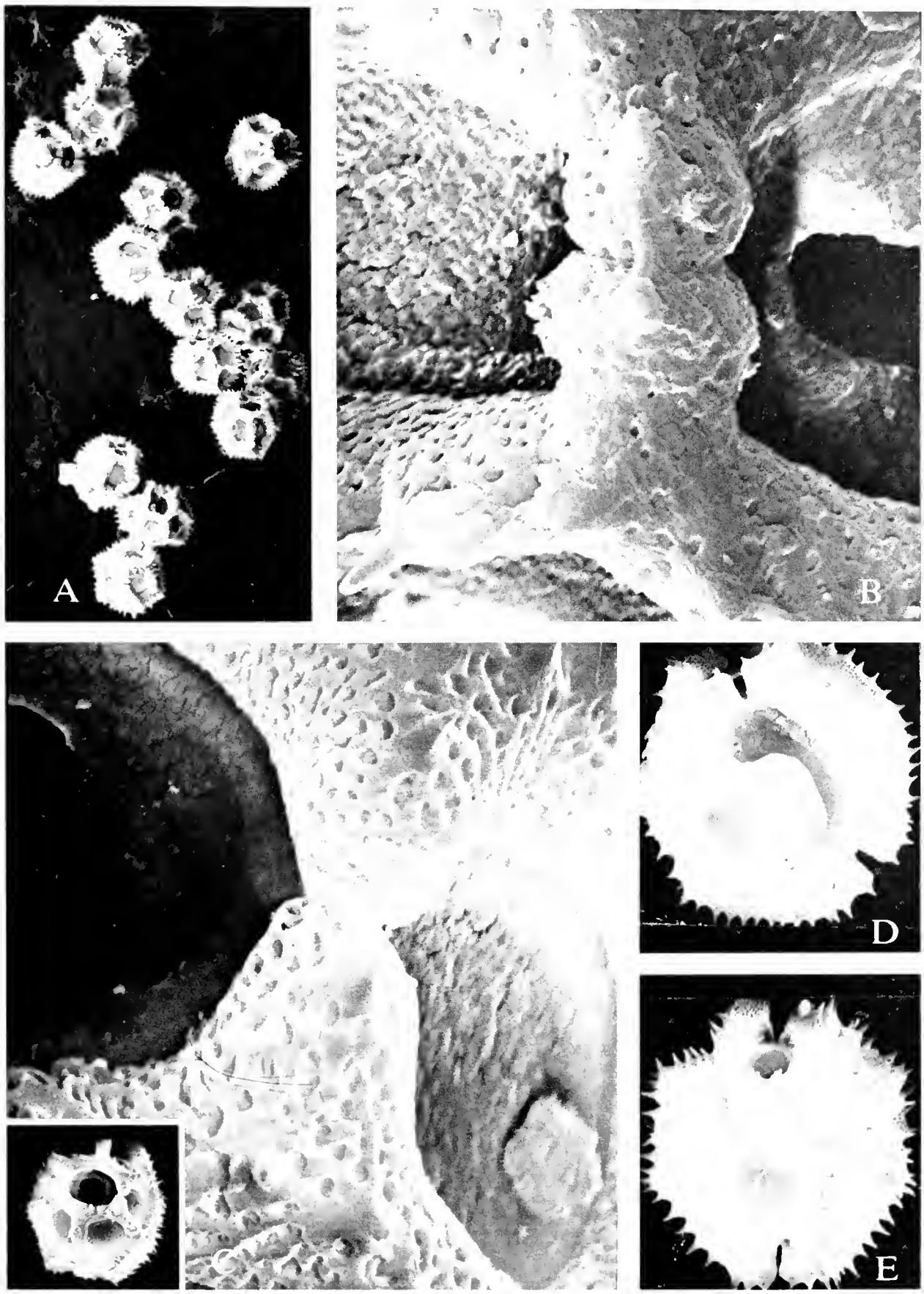
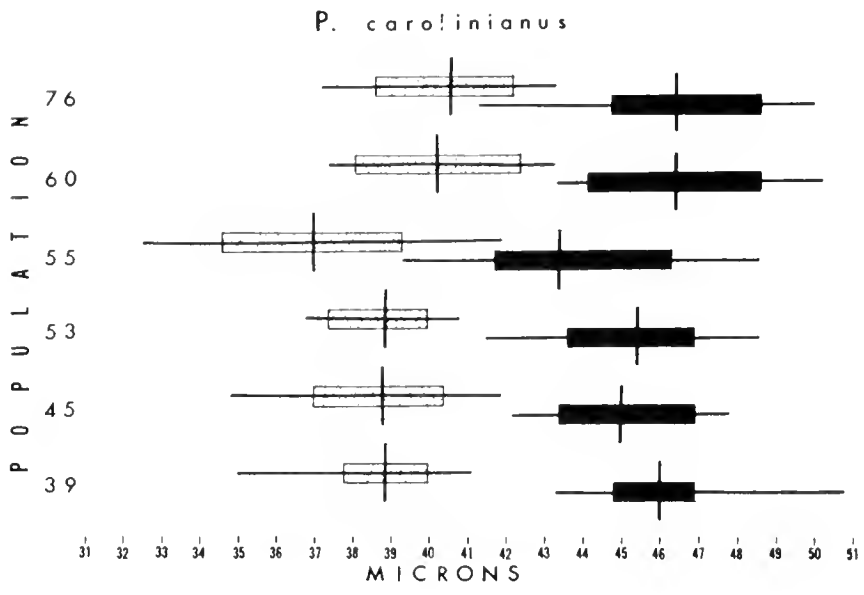
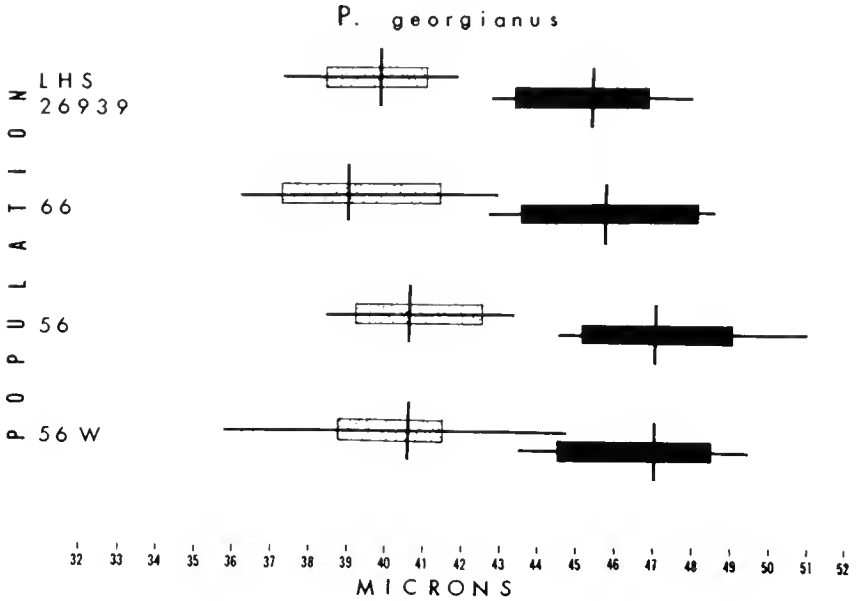
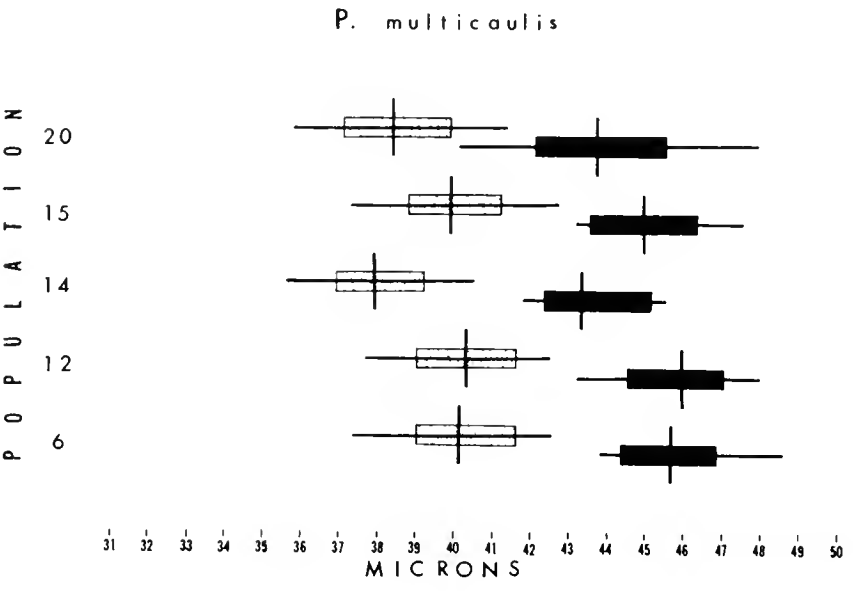


FIG. 1.—Scanning electron micrographs of *Pyrrhopappus* pollen grains: A, *P. carolinianus*, $n = 6$, showing echinolophate, tricolporate grains (about 300×); B, *P. carolinianus*, $n = 6$, showing detail of aperture area (about 7800×); C, *P. grandiflorus*, $n = 12$, showing entire pollen grain (inset) and detail of aperture area (inset about 580× and enlargement about 7500×); D, *P. grandiflorus*, $n = 12$, tricolporate grain (about 1025×); and E, *P. grandiflorus*, $n = 12$, tetracolporate grain (about 1025×).


P. carolinianus
POPULATION
76
60
55
53
45
39
31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51
MICRONS


P. georgianus
POPULATION
LHS 26939
66
56
56 W
32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52
MICRONS


P. multicaulis
POPULATION
20
15
14
12
6
31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50
MICRONS

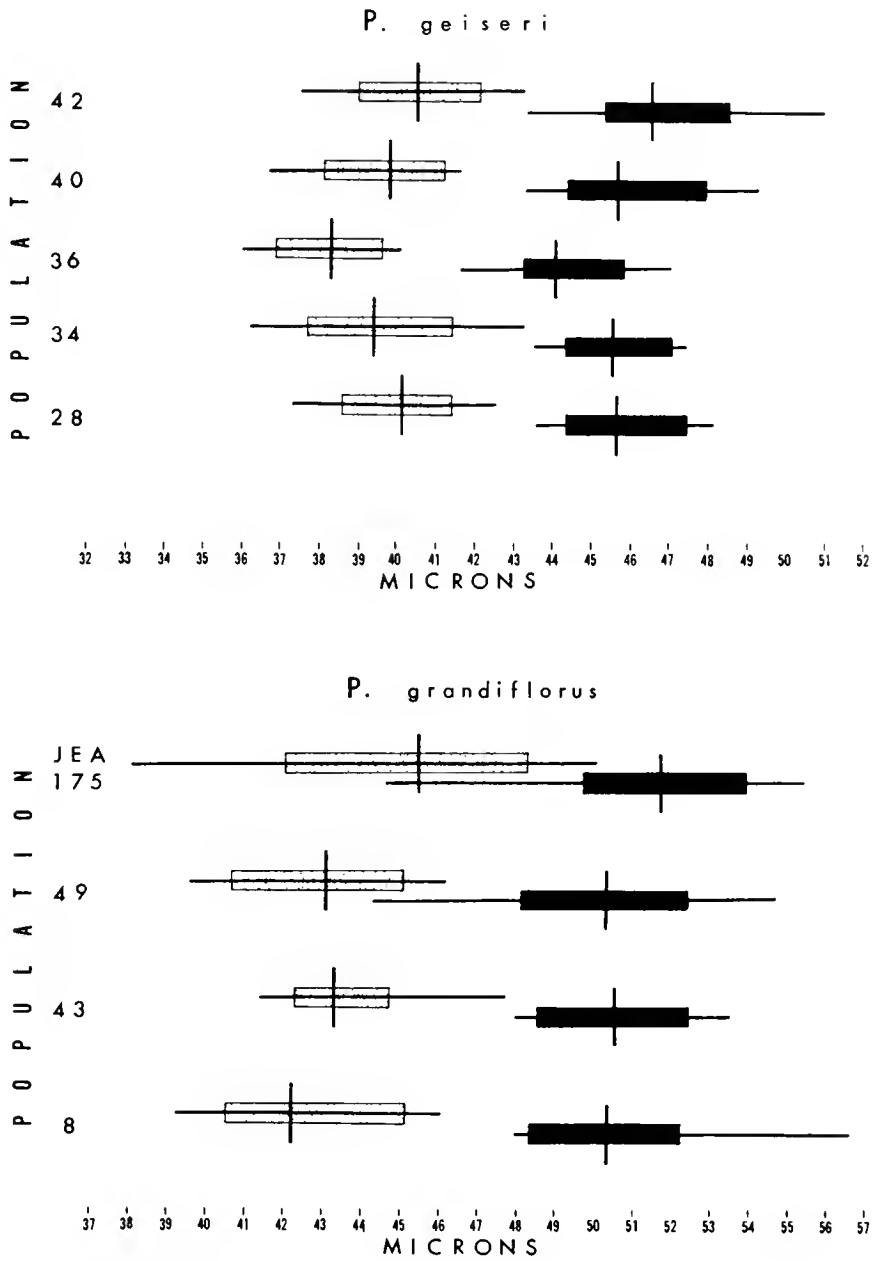


FIG. 2.—Graphic representation of pollen size for populations of five taxa of *Pyrrhopappus* (the two varieties of *P. multicaulis* are listed as *P. multicaulis* and *P. geiseri*). Localities for the population numbers are given in Table 2. The horizontal bars indicate range in size; vertical bars, means; and rectangles, two standard deviations (polar diameter of pollen grains is represented by stippled rectangles, and equatorial diameter by solid ones).

were softened in 10 per cent potassium hydroxide, then acetolyzed using the method described by Erdtman (1960). After acetolysis, the pollen was stained in 0.5 per cent safranin and suspended in 2000 cs silicone oil. From these suspensions, permanent slides were prepared on standard glass microscope slides with glass cover slips sealed with fingernail polish. Measurements and morphological descriptions were at 430× with a filar micrometer. Three measurements were made for each grain: 1) diameter in polar optical cross section to determine equatorial diameter (eq); 2) diameter in equatorial optical cross section to determine polar diameter (pl); and 3) spine length (sl). Approximately 50 grains were measured and averaged for each population. Measurements were made

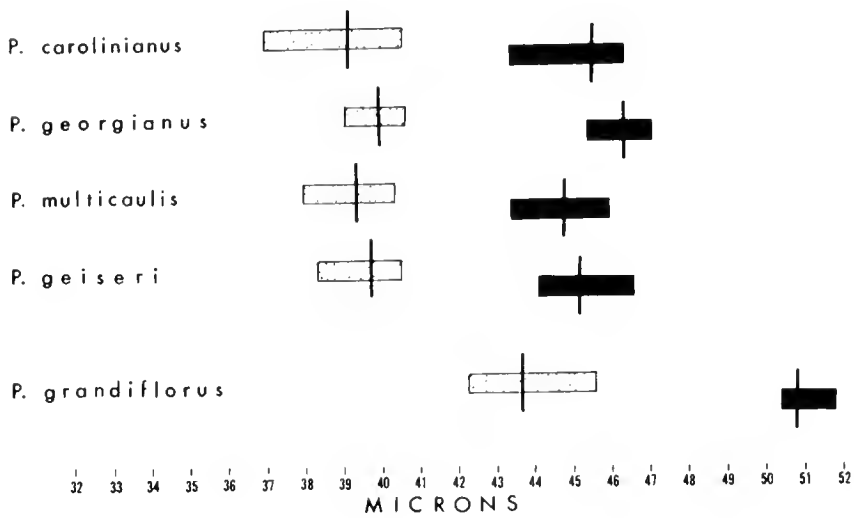


FIG. 3.—Graphic representation of population averages for pollen size in five species of *Pyrrhopappus*. Horizontal bars indicate means, and rectangles, ranges (polar diameter is represented by stippled rectangles, and equatorial diameter by solid ones).

from spine tip to spine tip. The morphology of the grains was noted using terminology proposed by Faegri and Iverson (1964).

Results.—The pollen of the four diploid taxa, *P. multicaulis*, *P. carolinianus*, *P. georgianus*, and *P. multicaulis* var. *geiseri*, are tricolporate and fenestrate with echinate sculpturing (termed echinolophate by Wodehouse, 1935). The grains are oblate, oval from the equatorial view and interhexagonal with intruding furrows from the polar view. In the tetraploid species, *P. grandiflorus*, however, both tri- and tetracolporate grains are found in approximately equal numbers in every population examined. Aside from possession of tetracolporate grains, *P. grandiflorus* is similar in pollen morphology to the diploid species. See Fig. 1.

Average pollen size in the several diploid species is quite similar, both within and between the populations comprising the taxa concerned (Figs. 2 and 3). The pollen of *Pyrrhopappus grandiflorus*, on the other hand, is substantially larger in both polar and equatorial diameters (Fig. 3). Thus, the tetraploid condition in *Pyrrhopappus* is characterized by increased pollen size and an additional morphological type, tetracolporate grains.

An examination of randomly selected tri- and tetracolporate pollen grains from three of the tetraploid populations revealed that pollen size is approximately the same in the two morphological types. Measurements from 20 grains of each type from each of the three populations showed that the size ranges and averages are essentially identical. Because of this, measurements on which the populational averages were based were made from grains selected randomly with no bias as to the number of apertures.

Discussion.—This investigation revealed a high degree of uniformity in morphology and size among the diploid species. For this reason, additional pollen study of the remaining diploid species was not undertaken. In contrast, the single tetraploid species possessed substantially larger pollen and a greater frequency of tetracolporate grains.

TABLE 1.—*Pollen grain measurements in microns.*

Taxon	Population	Average population measurements			Average
		pl	eq	sl	
P. carolinianus	76	40.6	46.4	2.88	
"	60	40.2	46.4	2.91	pl = 39.2
"	39	38.9	46.0	2.92	
"	53	38.9	45.4	2.42	eq = 45.6
"	45	38.8	45.0	2.84	
"	55	37.0	43.4	2.48	sl = 2.74
P. georgianus	56w	40.7	47.1	2.83	p = 40.0
"	56	40.7	47.1	2.76	
"	66	39.1	45.8	3.02	eq = 46.4
"	LHS 26939	39.9	45.4	2.76	sl = 2.84
P. multicaulis	12	40.4	46.0	2.87	pl = 39.4
var. *multicaulis*	6	40.2	45.7	2.68	
"	15	40.0	45.0	2.74	eq = 44.8
"	20	38.5	43.8	2.70	
"	14	38.0	43.4	2.70	sl = 2.74
P. multicaulis	42	40.6	46.6	2.96	p = 39.8
var. *geiseri*	28	40.2	45.7	2.92	
"	40	39.9	45.7	2.74	eq = 45.2
"	34	39.5	45.6	3.00	
"	36	38.4	44.1	2.64	sl = 2.85
P. grandiflorus	JEA				
"	175	45.6	51.8	2.98	pl = 43.7*
"	43	43.4	50.6	3.09	
"	49	43.2	50.4	2.94	eq = 50.8*
"	8	42.3	50.4	2.91	
"	48	38.4	46.6	2.94	sl = 2.97*

*The average sizes for *P. grandiflorus* were computed excluding population 48 (for explanation, see text).

The positive correlation of pollen dimorphism and polyploidy has been demonstrated by a number of workers. For example, Lewis (1964) found an increase in mean pollen sizes for known tetraploid populations above that of known diploid populations of *Oldenlandia corymbosa*. The tetraploid collections also showed a substantial number (36.9 per cent) of 4-aperturate grains in addition to the 3-aperturate condition, the latter occurring almost exclusively in the diploid collections of the same taxon. Similar results from other studies provide strong documentation for this phenomenon (Chuang and Constance, 1969; Lewis, W. H., 1965; Maurizio, 1956). Thus, in many reported cases, plants of higher ploidy levels are characterized by increased pollen size and aperture number.

Population 48 contains both tri- and tetracolporate pollen, but the average grain size is more like that of the diploid taxa. It should be noted that this pop-

ulation contained several atypical plants, the latter resembling putative triploid (F_1) intermediates between *Pyrrhopappus grandiflorus* and *P. multicaulis* var. *geiseri* (see section on chromosomal studies). As no chromosome counts were obtained from this population, the ploidyl level of these few aberrant plants is not known, but if the pollen material was indeed obtained from triploid F_1 individuals the reduced size would be expected. This expectation is based on pollen viability studies of known triploid populations, wherein a large number of grains showed a size range similar to that of diploid pollen. This was true of both the tri- and tetracolporate grains. Pollen size in the triploid material was that of normal tetraploid grains, with most of the larger grains viable (see section on chromosomal studies). Because of the likelihood of hybridization in population 48, data from this population were not used in the computation of average pollen sizes for *Pyrrhopappus grandiflorus* (Table 1).

On the generic level, the fenestrate condition in pollen development is believed to be highly derived and to stem from pollen types with a complete tectum (Faegri and Iverson, 1964). The regular pattern formed by the ridges is produced by the presence of gaps in the exine, termed lacunae. Because the Cichorieae are considered highly evolved by many workers, the fenestrate condition is consistent with such a view.

Specimens examined.—The locality, followed by the collector's name and catalogue number and institution of deposition, for specimens used as a source of pollen are listed below for each species.

Pyrrhopappus carolinianus. FLORIDA: Calhoun Co., Hwy. 71 South, 1 mi. S Blountstown, Northington 60 (TEX). LOUISIANA: Calcasieu Par., I-10 at Louisiana-Texas state line, Northington 53 (TEX). MISSISSIPPI: Jackson Co., 8 mi. E Biloxi, ½ mi. W jct. hwys. 50 and 90, Northington 55 (TEX). OKLAHOMA: Canadian Co., ½ mi. N I-40 on Geary, Bridgeport exit, Northington 45 (TEX). TENNESSEE: Washington Co., 1511 Robin Hood Lane, Johnson City, Northington 76, $n=6$ (TEX), TEXAS: Collin Co., Tex. 24, 4 mi. W FM 1385, Northington 39 (UT).

Pyrrhopappus multicaulis var. *geiseri.* OKLAHOMA: Murray Co., Hwy. 77 N Davis, Northington 42 (TEX). TEXAS: Denton Co., Hwy. 77 at Sanger, Northington 40 (TEX); McCulloch Co., US 87, 15 mi. N Brady, Northington 28 (TEX); McLennon Co., I-35, 24 mi. N Waco, 2 mi. S Cobb Creek, Northington 36 (TEX); Travis Co., I-35, 1 mi. N Pflugerville exit, Northington 34 (TEX).

Pyrrhopappus georgianus. ALABAMA: Baldwin Co., Shinners 26939 (SMU); Mobile Co., W Mobile on 90E at jct. 90E, 90W and 45, Northington 56 and 56W (TEX). GEORGIA: McIntosh Co., US 17, 4 mi. S Savannah, Northington 66 (TEX).

Pyrrhopappus grandiflorus. OKLAHOMA: Blaine Co., Hwy. 80 North, Roman Nose State Park, Northington 48 (TEX); Cleveland Co., Pauline's Patch Rd., SE Norman; 3 mi. E old 77 and ½ mi. past jct. with 9, East on 77, Northington 43 (TEX); Woodward Co.; Hwy. 34-C, 2 mi. from entrance to Boiling Springs State Park, Northington 49 (TEX). TEXAS: Blanco Co., Ranch Rd. 167, 14 mi. S jct. with US 280 near Blanco, Averett and Watson 175 (TEX); Gonzales Co., Palmetto State Park, near pond at campsite, Northington 8 (TEX).

Pyrrhopappus multicaulis var. *multicaulis.* TEXAS: Bexar Co., I-35, S San Antonio, 1 mi. N Leon Creek, Northington 12 (TEX); Caldwell Co., jct. US 183 and Tex. 21, 10 mi. N Lockhart, Northington 6; Frio Co., South Oak and East Frio Streets in Pearsall, Northington 14 (TEX); Gonzales Co., St. Lawrence and Fair Streets, Northington 20 (TEX); Live Oak Co. US 281, 6 mi. S Three Rivers, Northington 15 (TEX).

Chromosomal Studies

Relatively few chromosome counts had been reported for *Pyrrhopappus* prior to this study. Stebbins *et al.* (1953) reported somatic counts of $2n=12$ for *P. carolinianus* and *P. rothrockii*, Turner and Ellison (1960) obtained a meiotic count $n=6$ for *P. multicaulis* and Jones (1968*a*) reported *P. carolinianus* as $n=6$. This study had as its goal the establishment of chromosome counts from throughout the range of each taxon, and the examination of chromosomal morphology from karyotypes of each taxon.

Materials and methods.—Heads for meiotic counts were collected in the field, fixed in a modified Carnoy's solution (4 parts chloroform to 3 parts absolute alcohol to 1 part glacial acetic acid) and kept refrigerated until used. These were generally "populational" collections (*i.e.* buds from a number of plants in any one population were placed in a vial and examined until an unequivocal count might be made); however, in some areas containing putative hybrids or seemingly aberrant forms, individual plants were sampled. Material stored under refrigeration yielded counts for as long as two years, although progressive hardening of the meiotic cells with time made the longer-stored material difficult to handle. Counts were made more consistently and readily from material collected during the morning hours than from those collected in the afternoon or evening. Meiotic counts were obtained using the acetocarmine squash technique, with chromosomes examined from diakinesis through late anaphase. The most satisfactory stage for obtaining counts was metaphase or early anaphase.

Mitotic chromosomes were studied from root tip cells obtained from freshly germinated seed material. Achenes were washed in running tap water for approximately 24 hours, allowed to dry at room temperature for several days, and washed in 1.0 per cent chlorox for one minute. The achenes were then placed in petri dishes on either water agar or double-layered filter paper, which was initially flooded with distilled water. Approximately 50 per cent germination was obtained within one week.

One to three-day seedlings were submerged for about 90 minutes in a saturated aqueous solution of paradichlorobenzene at room temperature. The root tips were excised and stained in aceto-orecin (Tjio and Levan, 1950). Voucher specimens have been placed in the University of Texas Herbarium.

Results.—Chromosome counts were obtained for all six taxa. Altogether, 118 counts were obtained from 101 populations throughout the range of the genus (Grashoff *et al.*, 1972). *P. carolinianus*, *P. multicaulis* var. *multicaulis*, and *P. rothrockii* are diploid, $n=6$. In addition, counts of $n=6$ were obtained for *P. georgianus* and *P. multicaulis* var. *geiseri*. The remaining taxon, *P. grandiflorus*, is $n=12$. See Fig. 4.

In a region of sympatry between *P. grandiflorus* and *P. multicaulis* var. *geiseri*, populations were found that contained triploids with $2n=18$. In some populations, both parental species were present in addition to the morphologically intermediate, putatively hybrid triploids. In such populations, diploid and tetraploid counts were obtained from *P. multicaulis* var. *geiseri* and *P. grandiflorus* respectively. Within other populations, however, the morphology of the triploid

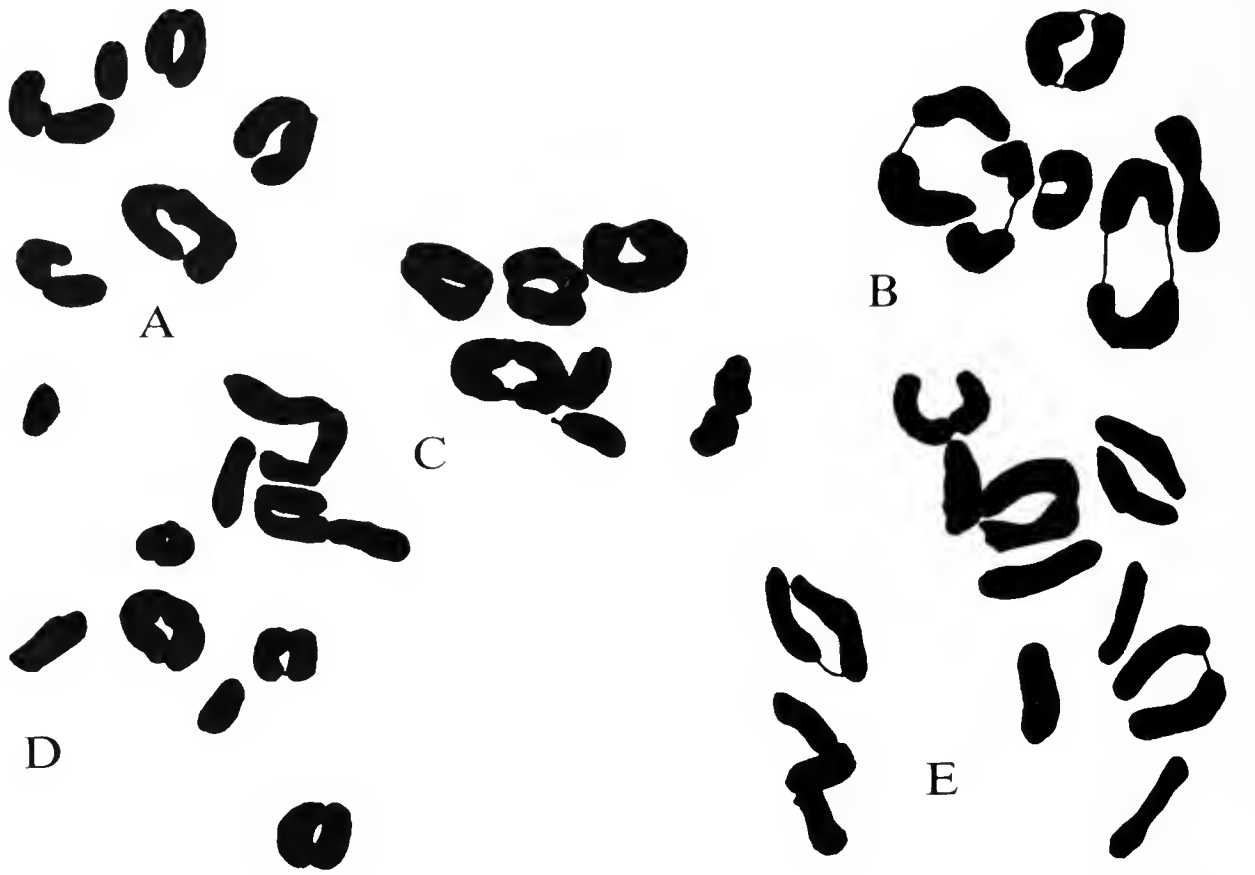


FIG. 4.—Camera lucida drawings of chromosomes of *Pyrrhopappus*: A, *P. multicaulis* var. *multicaulis*, $n = 6$, metaphase I (Northington 6); B, *P. georgianus*, $n = 6$, early anaphase I (Northington 197); C, *P. multicaulis* var. *multicaulis*, $n = 6$, metaphase I (Tomb 358); D-E, *P. grandiflorus* × *P. multicaulis* var. *geiseri* putative triploid hybrid, $2n = 18$, metaphase I (Northington 85c). All drawings are approximately 860×.

individuals approached that of *P. grandiflorus* more closely than that of *P. multicaulis* var. *geiseri* (Fig. 5); careful examination of such populations revealed only triploid individuals.

Four of the latter populations were encountered that were initially thought on the basis of morphology to be composed entirely of *P. grandiflorus*. Upon careful examination, however, characters not usually associated with the tetraploid plants in a "pure" population were noted. In each triploid population, counts were obtained from bud material from 10 to 15 different plants with 10 or more countable cells observed from each preparation before the count was considered positive. Because of the above mentioned morphological structure of the population, it is not certain that tetraploid plants were absent, but if present, they were not readily recognizable by their morphology and were certainly far fewer in number than the triploids. There was no evidence, either morphological or chromosomal, that the diploid, *P. multicaulis* var. *geiseri*, occurred in such populations.

An examination of pollen viability in three triploid populations (one having both parental species present, the other two having only triploid individuals), revealed pollen viability of 25, 18, and 25 per cent, respectively. These percent-

FIG. 5.—Camera lucida drawings of chromosomes of *Pyrrhopappus* (*P. grandiflorus* × *P. multicaulis* var. *geiseri* putative triploid hybrids at metaphase I): A, $2n = 18$ (Northington 221); B, $2n = 18$ (Northington 228). Both drawings are approximately 1940×.

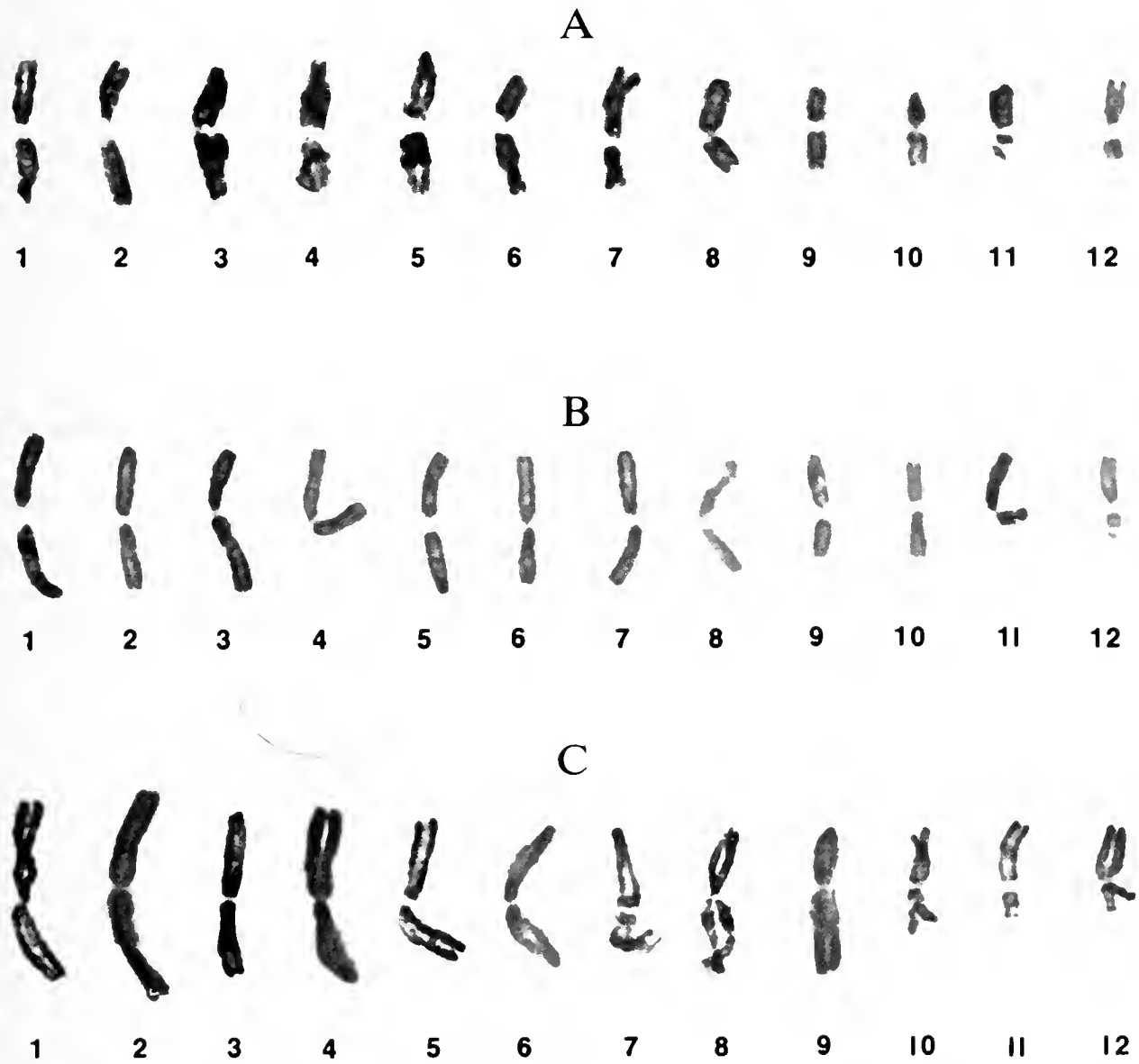


FIG. 6.—Karyotypes of *P. georgianus* and *P. carolinianus*: A, *P. georgianus*, primary root tip, Northington 187 (about 860×); B, *P. georgianus*, primary root tip, Northington 192 (about 940×); C, *P. carolinianus*, primary root tip, Northington 76 (about 1000×).

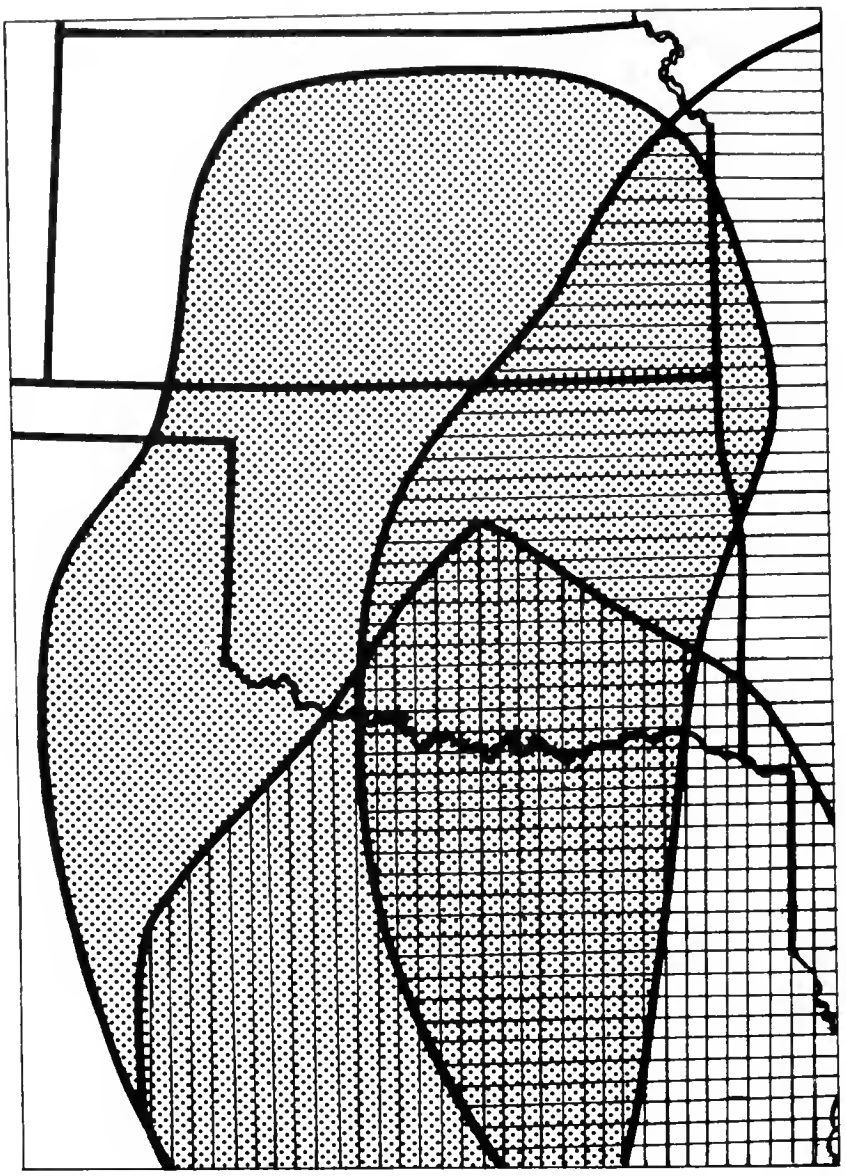


FIG. 7.—Map outlining the areas of sympatry between: A, *P. carolinianus* (horizontal lines); B, *P. multicaulis* (vertical lines); and C, *P. grandiflorus* (stippled).

ages were based on an examination of 400 grains per population stained with lactophenol blue.

Examination of mitotic cells from root tip preparations yielded counts of $2n = 12$ for several of the diploid taxa. In addition, chromosome morphology in two of the taxa, *P. carolinianus* and *P. georgianus*, was established (Fig. 6). In both taxa, one pair of chromosomes had satellites and subterminal centromeres, whereas the remaining chromosomes had median or submedian centromeres and were without satellites. The chromosome sizes were comparable in the two taxa, with four pairs being larger than the other two and the satellited pair always being the shortest of the set. These results are similar to those obtained by Stebbins *et al.* (1953), except that their figure 16, showing a camera lucida of the chromosomes of *P. carolinianus*, illustrated one of the larger chromosome pairs as bearing satellites. To date, I have not found satellites on any of the chromosomes other than the previously mentioned smallest pair.

Discussion.—Chromosomal studies have contributed relatively little to this study at the specific level or lower. That the genus is a closely knit group, however, is supported by the monobasic ($x = 6$) condition. From morphological and chemical data (discussed elsewhere), the tetraploid is believed to be of relatively ancient origin and is probably not derived from extant taxa. However, *P. grandiflorus* shows a greater morphological similarity to *P. multicaulis*, especially at the juvenile stage, than to any other existing taxon.

The distribution of *P. grandiflorus*, while centered in north-central Texas and Oklahoma, extends into that of the more southern *P. multicaulis*. Based on distribution and morphology, then, the tetraploid taxon could conceivably have arisen by autopolyploidy from *P. multicaulis* or a progenitor of that taxon. However, inasmuch as the distribution of *P. grandiflorus* is somewhat peripheral to the area of sympatry between *P. multicaulis* and *P. carolinianus* (Fig. 7), the possibility of an allopolyploid origin from these two diploid taxa or their progenitors must also be considered.

Hypotheses for either the auto- or allopolyploid origins of *P. grandiflorus* can be supported by the assembled data in Table 2. Based primarily on the cytological evidence, it is more probable that *P. grandiflorus* is of ancient allotetraploid origin. Experimental hybridization studies might help resolve the problem; however, considering its likely age as judged by its morphological divergence from related taxa, the origin of *P. grandiflorus* may never be determined conclusively.

As noted, when *P. grandiflorus* and *P. multicaulis* var. *geiseri* grow together at a given site, the occurrence of triploid F_1 hybrids can be expected. The regularity of this event indicates that some similarity must exist between at least one set of genomes in the two species and furnishes additional evidence for the close relationships among all the taxa in the genus.

Whatever the origin of the tetraploid species, the "stabilized" triploid could be a result of the "self cleaning" phenomenon (Lewis, 1967) in which the successful invasion of a tetraploid population by a diploid one is prevented. The absence, or at least the greatly reduced number, of tetraploid plants is more difficult to explain. Again, according to Lewis, "If a diploid should become established within a tetraploid population the progeny will mostly be triploid. Should a triploid become established in the midst of the tetraploids its progeny will either be tetraploid or triploid." If a triploid-tetraploid cross would produce significantly more triploid than tetraploid individuals, and the same result were to stem from triploid-triploid crosses, a much higher frequency of triploid than tetraploid progeny would be expected. Additional populational study and experimental work might help answer this question, but a certain degree of triploid viability must be present.

Although a pollen viability rate lower than about 40 per cent might be considered equivalent to "sterility," the established range of 18 to 25 per cent mentioned earlier certainly does not preclude the ability of triploids to produce offspring. In fact, it has been demonstrated by Lewis (1967) that occasional viable plants are produced from triploid individuals having a much lower stainability.

TABLE 2.—*Summary of evidence supporting either allopolyploidal or autopolyploidal origin of* P. grandiflorus.

Allopolyploidy	*Autopolyploidy*
1. Morphology:	1. Morphology:
a. *P. grandiflorus* is a morphologically distinct species.	a.
b.	b. *P. grandiflorus* is similar in many characters to the diploid *P. multicaulis*, especially in the juvenile state.
c.	c. *P. grandiflorus* possesses enlarged morphological features such as head, peduncle, and pollen that are often associated with autopolyploidy.
2. Distribution: *P. grandiflorus* extends between the range of *P. carolinianus* and *P. multicaulis* north and west into what might have once been newly available habitats.	2. Distribution: *P. grandiflorus* extends from well within the range of *P. multicaulis* north and west into what might have once been newly available habitats.
3. Cytogenetics:	3. Cytogenetics:
a. Meiotic pairing in *P. grandiflorus* is regular with 12 bivalents and no multivalents.	a.
b. Meiotic configurations in the F_1 triploids found in natural populations is composed of two trivalents, four bivalents, and four univalents in more than 80% of the cells examined. This consistently low number of trivalents would be expected in a triploid derived from an allotetraploid-diploid cross.	b.

FLAVONOID STUDIES

Materials and methods.—In examining the inter- and intrapopulational variation of flavonoid compounds for each taxon of *Pyrrhopappus*, plants were selected from throughout as much of the range as available time and opportunity permitted. In each population, two to five plants were sampled, these yielding four to 10 sheets of chromatographic patterns. Chromatographic profiles of the compounds present in each population were used in analyzing interpopulational variation. Vouchers for all populations sampled are in the University of Texas Herbarium.

Standard two-dimensional, paper chromatographic techniques were used to achieve compound separation and pattern analysis, (Mabry *et al.*, 1970). The flavonoid compounds were extracted from dried leaf materials selected from

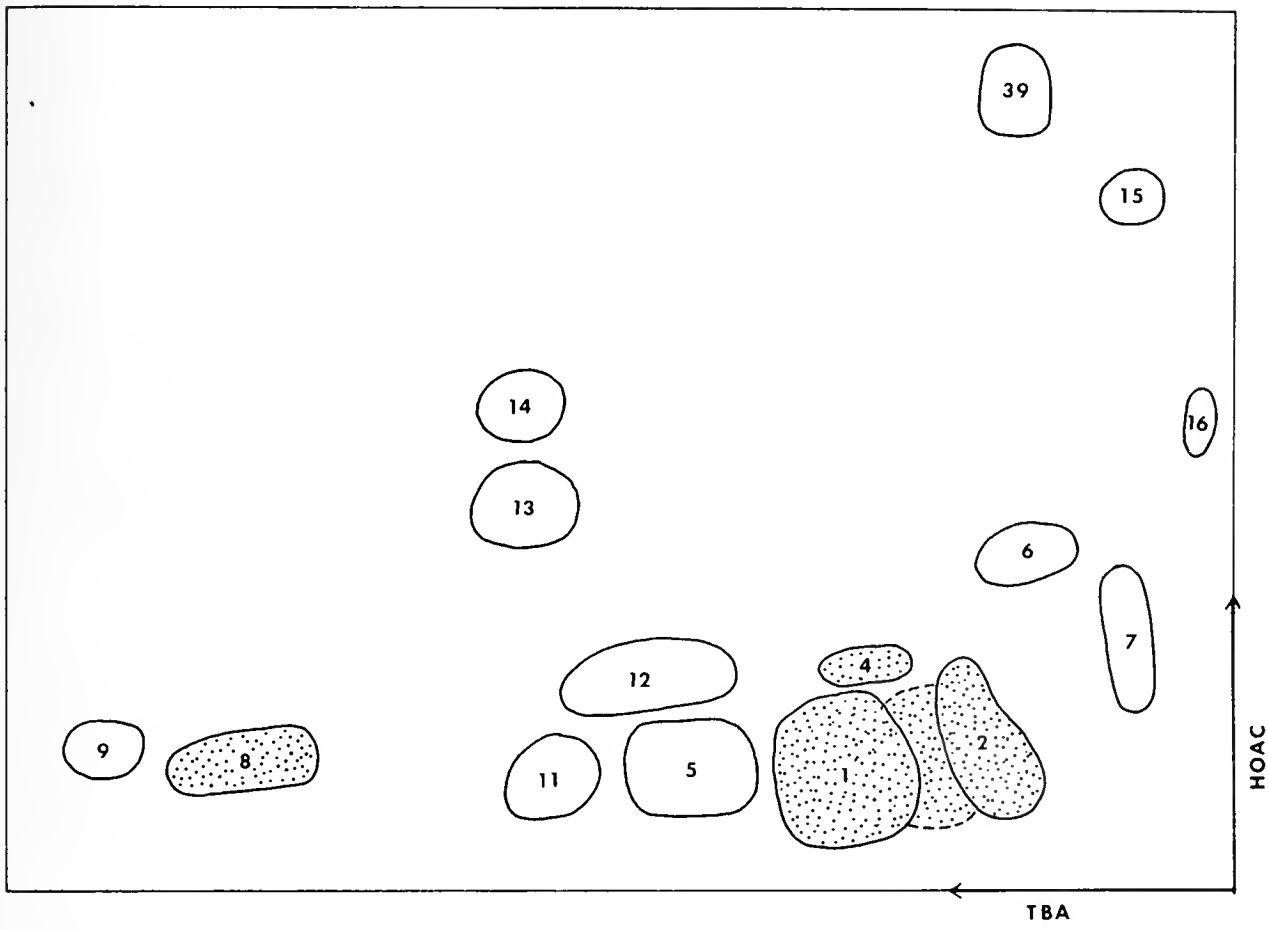


FIG. 8.—Composite chromatographic profile for all taxa of *Pyrrhopappus*. Stippled areas indicate those compounds present in all taxa.

mature leaves at approximately the same developmental stage. The extract was "spotted" on Whatman 3MM chromatographic paper and developed in two solvent systems: tertiary butanol, glacial acetic acid, and water (3:1:1 v/v) and 15 per cent glacial acetic acid, referred to as TBA and HOAC respectively. The dried chromatograms were observed over ultraviolet light before and after exposure to ammonia vapor to establish both the positions of the various compounds and their color characteristics on the paper.

The technique used for the ultraviolet spectral analysis of flavonoid compounds was that of Mabry *et al.* (1970), with the exception that fused sodium acetate was used. For glycosidic compounds, acid hydrolysis was employed to obtain the aglycone for positive identification via cochromatography and to establish the nature of the glycoside(s) present. Acid hydrolysis was achieved by refluxing the compound in 5 per cent HCL (approximately 75° C) for about one hour. The resultant sugar was either eluted directly with water or separated from the aglycone by using a water-ethyl acetate solution in a separatory funnel. The resultant sugar was spotted on paper with known sugars for comparison by one-dimensional chromatography developed in ethyl acetate, pyridine, and water (12:5:4 v/v). This chromatogram was subsequently dried, sprayed with P-anisidine hydrochloride (three per cent) in n-butanol (Mann Research Laboratories, N.Y.), and oven dried at 130° C for 10 minutes. Sugars were visible as yellow to brown spots.

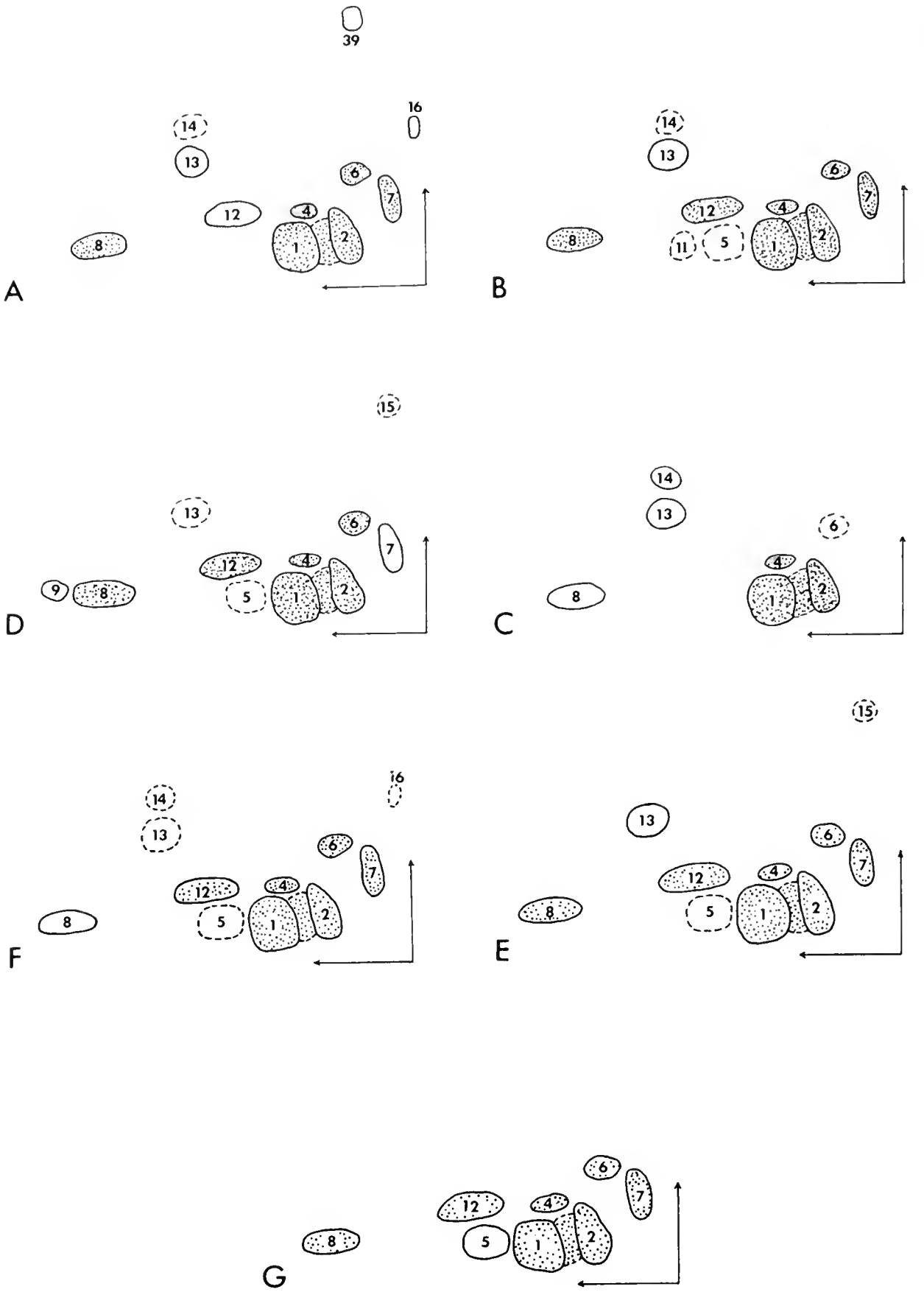


FIG. 9.—Chromatographic profiles of *Pyrrhopappus* taxa: A, *P. rothrockii*; B, *P. georgianus*; C, *P. grandiflorus*; D, *P. carolinianus*; E, *P. multicaulis* var. *multicaulis*; F, *P. multicaulis* var. *geiseri*; G, populations of cream-colored heads of reduced size discussed in the section on populational studies.

TABLE 3.—*Identity and chromatographic properties of the flavonoids of* Pyrrhopappus: *purple; Y, yellow; Y/GR, yellow-green.*

Identity	Color		*Rf* values	
	UV	+NH3	TBA	HOAC
1. Luteolin 7-0-glucoside	P	Y	.38	.16
2. Luteolin 7-0-diglucoside	P	Y	.23	.20
3. Luteolin	P	Y	.73	.06
4. Apigenin 7-0-monoglycoside	P	Y/Gr	.35	.29
12. Apigenin 7-0-monoglycoside	P	Y/Gr	.51	.27
9. Apigenin	P	Y/Gr	.82	.09

Results.—All flavonoid compounds present in the various taxa of *Pyrrhopappus* are represented in the composite chromatogram (Fig. 8). Each spot is numbered for convenience of discussion, and compounds from different taxa designated by the same number are considered chemically identical. Such an assumption is supported by cochromatography. Those compounds for which enough material was available were identified to their base structure by spectral methods. Those flavonoids identified to date in *Pyrrhopappus* have all been flavones and have either luteolin or apigenin as their skeletal structures. Table 3 lists by number the chromatographic data for these compounds and their identity.

These compounds are represented in Fig. 9 by spots indicating their percentage occurrence within the various populations sampled for each taxon. Those compounds outlined with a solid line and shaded within occurred more than 90 per cent of the time, solid lines without shading occurred from 35 to 85 per cent of the time, and dotted lines indicate occurrence of 30 per cent or below. For comparisons between taxa, only compounds indicated by solid lines are considered unless otherwise stated. Inasmuch as the process of identification is similar for each compound, an example of spectral data analysis will be demonstrated in detail only for compound 1. The absorption maxima (λ max) for all compounds examined spectrally are presented in Table 4.

The initial chromatographic information for compound 1 (*i.e., Rf* value and color/color change with NH_3) indicates, as shown in Table 3, either a flavone with a hydroxyl at the 5 and 4′ positions or a 3 —OH substituted flavonol with a 5 and 4′ —OH. In either case, the compound is likely a 7-0-monoglycoside. Determination of the actual substitutions for each position is made by examining the wave length shifts with various reagents. The spectral data obtained using spectral methanol serve as a reference for the other reagents, and the λ max for band I of 350 nanometers is within the range of flavones. A bathochromic (higher wave length) shift of 56 nm. in sodium methoxide with no decrease in intensity indicates a 4′ hydroxyl group. The absence of a decrease in peak in-

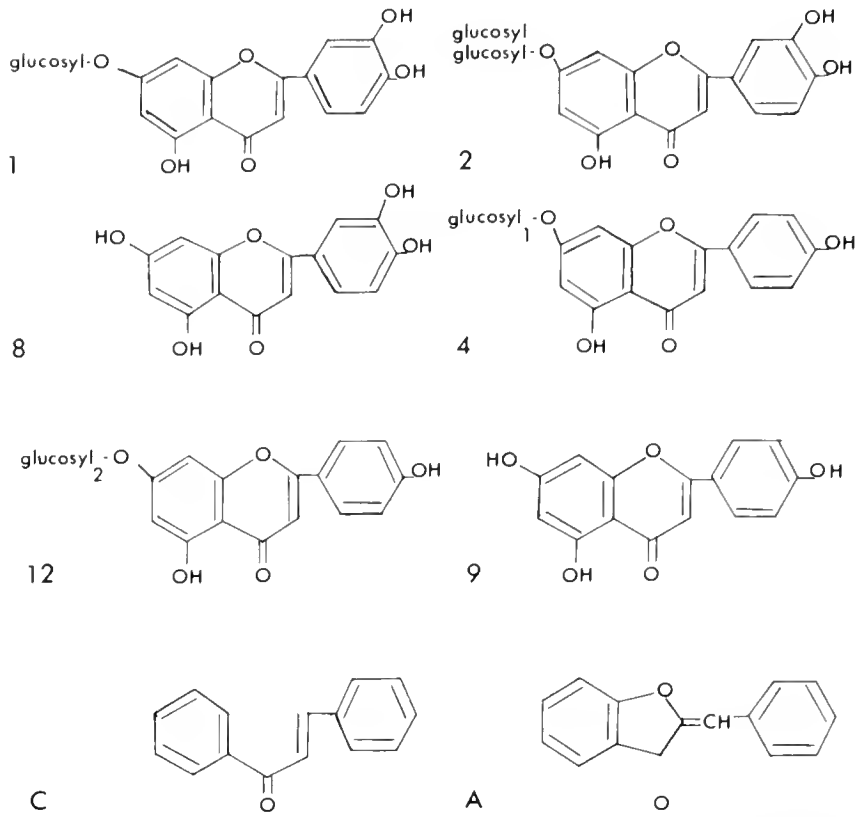


FIG. 10.—Structures of the identified flavonoid compounds in *Pyrrhopappus* (numbering and lettering are consistent with that in Tables 4 and 5): 1, luteolin 7-0-glucoside; 2, luteolin 7-0-diglucoside; 4, apigenin 7-0-glucoside$_1$; 8, luteolin; 9, apigenin; 12, apigenin 7-0-glycoside$_2$; C, chalcone base skeletal structure; and A, aurone base skeletal structure.

tensity and the fact that compound 1 appears purple under ultraviolet light indicates the lack of a hydroxyl group at position 3. In aluminum chloride, a shift of 80 nm. was observed. This shift indicates the presence of both a 5 hydroxyl group that forms a complex with the carbonyl group producing a 45-nm. shift and an ortho dihydroxyl complex at the 3′ 4′ position that produces a 35-nm. shift. Shifts of the 5 hydroxyl and the ortho dihydroxyl complexes are additive, thus the 80-nm. shift observed. The hypsochromic (lower wave length) shift of 42 nm. produced by the addition of HCL to the solution containing aluminum chloride is a result of the destruction of the complex formed at the 3′, 4′ ortho dihydroxyl position, thus verifying its presence. In sodium acetate, a bathochromic shift of 5 to 20 nm. would be expected if there were a hydroxyl group at the 7 position, therefore, the 4-nm. shift observed with this reagent indicates the absence of hydroxyl at the 7 position. Boric acid added to the sodium acetate complex is used for the detection of ortho dihydroxyls, and the shift of 23 nm. is well within the expected 15 to 25-nm. shift range when an ortho dihydroxyl is present, thus, further verifying earlier data to this effect.

The spectral data above, therefore, indicate compound 1 to be a flavone with a 3′, 4′ ortho dihydroxyl, a 5 hydroxyl, with the 7 position substituted. The chromatographic data suggest the substitution at the 7 position to be an 0-monoglycoside.

Identification of the sugar moiety of compound 1 was accomplished by acid hydrolysis. By this method, the aglycone, luteolin, was obtained, and the sugar spot on the one-dimensional chromatogram ran the same distance as the known sugar, glucose. Identification of the aglycone was accomplished by cochromatography with a known standard sample of luteolin. The final identification of compound 1, then, is luteolin 7-0-glucoside (Fig. 10).

For compound 2, the spectral data are virtually identical to those for compound 1, and acid hydrolysis yields glucose as the only sugar present. An interesting point concerning the acid hydrolysis of compound 2 is that much less sugar was obtained by this method than from compound 1. Initially, this led to confusion, as a diglucoside was suspected, and if this were so, a greater quantity of sugar would be expected following hydrolysis. In checking the aglycone, three spots were observed: the expected aglycone, luteolin, and two faint spots in the same positions as the glycosidic compounds 1 and 2. Thus, incomplete hydrolysis of the sugar moiety resulted in the appearance of both the mono- and diglycoside, in addition to the aglycone.

Based on this information and the fact that diglycosides run slower in TBA and faster in HOAC than do their corresponding monoglycosides, the *Rf* value of compound 2 strongly suggested luteolin 7-0-diglucoside. The colored area detectable between spots 1 and 2 is probably an artifact, *i.e.*, an area where the mono- and diglucosides have lost or gained a glucose while developing in the solvent systems.

For compound 8, in addition to its chromatographic properties and cochromatography with stock luteolin, ultraviolet spectral data were obtained that matched the λ max data of a known standard luteolin. Compound 8, then, is luteolin.

In addition to the luteolin series, *Pyrrhopappus* has flavone compounds with a different base skeleton, apigenin. Based on *Rf* values, both number 4 and 12 are probably monoglycosides and ultraviolet spectral data for both are very close to those of apigenin 7-0-glucoside. Difficulty in obtaining the sugar moiety by acid hydrolysis has thus far prevented absolute identification; however, an aglycone was obtained from the hydrolyses of both compounds, indicating that a sugar was, in fact, removed, although no spot was obtained from the one-dimensional sugar chromatogram in either case. As the spots 4 and 12 occur in weak density relative to spots 1 and 2, only a few attempts to obtain the hydrolyzed sugar were possible; all produced identical results as stated.

Cochromatography of the two aglycones obtained from compounds 4 and 12 with both spot 9 and a standard apigenin sample established the four compounds to have the same chromatographic properties. As the lack of material precluded ultraviolet spectral examination of compound 9, its identity as apigenin is based on these chromatographic properties. Compounds 4 and 12, then, are felt to be apigenin 7-0-monoglycosides, and the difference in TBA *Rf* value probably results from differences in their respective sugars.

Compounds 6 and 7, although occurring with regularity, were usually so faint as to make extremely difficult the elution of enough material from paper on which to run ultraviolet spectra. Although enough material was possibly obtained,

TABLE 4.—*Absorption maxima of the flavonoids of* Pyrrhopappus.

	MeOH	NaOMe	$AlCl_3$	$AlCl_3$/HCl	NaOAc	H_3BO_3
1.	254, 264sh, 350	263, 293sh, 397	273, 290sh, 328, 430	270, 293sh, 361, 338	258, 265sh, 407	259, 374
2.	255, 265sh, 350	265, 295sh, 406	274, 290sh, 328, 429	265, 295sh, 366sh, 388	258, 265, 407	258, 373
8.	250, 270 284sh, 348	272, 326sh, 407	271, 303sh, 328, 423	274, 292sh, 350, 384	270, 324sh, 398	257, 302sh 370, 425sh
4.	255, 327	270, 297sh, 391	272, 295, 346, 383	272, 295, 338, 378	353sh, 386	265sh, 327
12.	253, 324	270, 295sh, 390	271, 295sh, 343, 377	270, 295sh, 338, 377	265, 350, 387	265, 342

efforts to reduce paper contamination by respotting and redeveloping in greater concentrations met with virtually the complete loss of both compounds.

Compounds 5, 11, 13, 15, and 16 all occur very seldom and in very weak concentrations, which precludes identification based on ultraviolet spectral data. Compound 39 is a pink spot that, although not a flavonoid, is included on the chromatographic profile of *P. rothrockii* because it serves as a convenient marker, inasmuch as it is both consistently present and unique to this taxon.

Common to all the taxa of *Pyrrhopappus* are two compounds obtained in extracts from the ligules. These compounds produce bright yellow spots that turn red or orange-red on exposure to ammonia vapor, a unique characteristic of a class of flavonoid compounds often referred to as anthochlor pigments. These pigments are of two structural types, chalcones and aurones (see Fig. 10 for their respective chemical skeletons). Attempts at identification of these compounds through ultraviolet and nuclear magnetic resonance spectroscopy have not as yet been fruitful.

The interesting fact concerning the occurrence of anthochlor pigments in the ligules of *Pyrrhopappus* is that they have not been reported in any other member of the tribe Cichorieae. Nearly all reports of anthochlor pigments in Compositae have been for members of the tribe Coreopsidineae, especially the genus *Coreopsis* (Harborne, 1967). Thus, the mere existence of these compounds in *Pyrrhopappus* is of considerable interest, and possibly taxonomically significant at the generic level or higher.

Dicussion.—The chromatographic data obtained for the various taxa of *Pyrrhopappus*, although very consistent intrapopulationally, exhibited some variability from population to population within each taxon. In addition, the entire genus exhibits a strong flavonoid unity as demonstrated by the high degree of pattern similarity among taxa. Nevertheless, species-specific patterns do exist and they indicate the same trends as do morphological data. For example, *P. multicaulis* var. *multicaulis* and *P. m.* var. *geiseri* (Fig. 9) have the same compounds in common if only those compounds occurring consistently are considered (see

p. 19 for an explanation of compound occurrence as shown by the figures of chromatographic patterns).

Between the morphologically distinct taxa, *P. multicaulis* and *P. carolinianus*, a consistent difference of one compound is found. Thus, *P. carolinianus* has compound 9 present more than 50 per cent of the time whereas compound 9 has not been detected in *P. multicaulis*. In addition, compound 13, although present in both taxa, occurs about 60 per cent of the time in *P. multicaulis* and less than 35 per cent of the time in *P. carolinianus*.

Comparing the closely related *P. georgianus* and *P. carolinianus*, the former lacks compound 9 whereas the latter possesses it consistently. In addition, *P. georgianus* occasionally has spot 14, which is always lacking in *P. carolinianus*; the reverse holds for spot 15, which is present occasionally in *P. carolinianus*, but absent in *P. georgianus*.

The very distinct taxon, *P. rothrockii*, differs from its most closely related taxon, *P. multicaulis*, by two compounds, 16, occurring in more than 60 per cent of *P. rothrockii* plants but not at all in *P. multicaulis*, and the pink spot, compound 39, which exists only in *P. rothrockii*.

Overall, *P. grandiflorus* has the most distinct flavonoid pattern in the genus. It possesses relatively few spots, lacking completely 5, 7, 9, 12, 15, and 16 and having spot 6 present only some of the time (Fig. 9). Because *P. grandiflorus* is tetraploid and "polyploid buffering" (Stebbins, 1950) would tend to prevent the loss of compounds, the most logical explanation for the reduced number of compounds in this species is that its polyploid nature is of ancient origin, and that the compounds possessed are those that formed the original flavonoid "gene pool" and were shared by the other species. The subsequent acquisition of compounds by the other (diploid) taxa could be explained by subsequent mutational events or by gene flow due to hybridization between closely related taxa within the genus. In *P. grandiflorus*, however, polyploid buffering would tend to prevent an increase or loss in flavonoid characters due to mutational events alone. This explanation would account for the reduced number of compounds in *P. grandiflorus* relative to the diploid taxa.

An examination of plants believed to belong to *P. multicaulis*, and bearing cream-colored heads of greatly reduced size was undertaken in an attempt to clarify the morphological data discussed in the section on populational studies. Flavonoid data showed such plants to differ from "typical" *P. multicaulis* by having neither compound 13 nor 15 (Fig. 9); more than half the typical *P. multicaulis* plants have 13 and fewer than one-fourth of them have 15. More data are necessary before these trends can be considered as more than suggestive. However, in comparison with the differences found throughout the genus, the cream-colored populations are believed to be more than regionalized color forms.

Although some species-specific trends in flavonoid chromatographic patterns do exist and serve to substantiate the relationships among the taxa based on morphological and other data, the most significant aspect of this work is the high degree of generic unity suggested by the flavonoids. Even the most distantly related species in the genus share with the other taxa a very similar flavonoid chem-

istry. The latter data should prove useful in future work at the generic or supra-generic level.

Specimens examined.—The locality for each voucher specimen, followed by the name and catalogue number of the collector, is listed below for species examined for flavonoids by paper chromatography. An asterisk denotes specimens collected from populations in south Texas with cream-colored, very reduced ligules (see section on Populational Studies).

Pyrrhopappus carolinianus. FLORIDA: Bay Co., Hwy. 231, 10 mi. S Bennett, Northington 58; Leon Co., jct. US 90 and Fla. 261, Northington 62. GEORGIA: Tift Co., US 82, 2 mi. W Tift-Berrien Co. line, Northington and Bierner 193. LOUISIANA: Acadia Par., I-10, 4 mi. W Crowley, Northington 54; Calcasieu Par., I-10 at Louisiana-Texas state line, Northington 53; St. Tammany Par., US 190, 8.5 mi. W jct. US 190 and US 11, Northington and Bierner 161. MISSISSIPPI: Harrison Co., US 90, 27.8 mi. E Louisiana-Mississippi state line in Gulfport, Northington and Bierner 164; Lafayette Co., 200 yds. W Hwy. 6W and Sorority Row, University of Mississippi Campus, Oxford, Northington 78. NORTH CAROLINA: Henderson Co., I-26 at Fletcher, Northington 73. OKLAHOMA: Canadian Co., ½ mi. N I-40 on Geary, Bridgeport exit, Northington 45. Tennessee: Washington Co., 1511 Robin Hood Lane, Johnson City, Northington 76. TEXAS: Bastrop Co., Bastrop State Park, Northington 216.

Pyrrhopappus georgianus. FLORIDA: Alachua Co., 4.4 mi. SW jct. Fla. 24 and US 301 on Fla. 24, Northington and Bierner 185; Bay Co., US 231, 3.3 mi. NE jct. US 231 and US 98, Northington and Bierner 173; Duval Co., 2.5 mi. NE jct. US 301 and I-10, Northington and Bierner 187; Gilchrist Co., 0.2 mi. E jct. US 129 and Fla. 26, Northington and Bierner 176; Liberty Co., Fla. 20, 2.1 mi. E jct. Fla. 20 and Fla. 65, Northington and Bierner 176; Okaloosa Co., US 90, 3.2 mi. E Crestview, Northington and Bierner 171; Taylor Co., 1.5 mi. SSE Salen on US 27 Alt, Northington and Bierner 181; Wakulla Co., 3.8 mi. S Leon-Wakulla Co. line on Fla. 363, Northington and Bierner 178. GEORGIA: Atkinson Co., US 82, 2.4 mi. W jct. US 82 and US 221, Northington and Bierner 192; Charleton Co., 5.4 mi. NW Georgia-Florida state line, Northington and Bierner 189; Ware Co., 10.8 mi. E Ware-Atkinson Co. line on US 82, Northington and Bierner 191.

Pyrrhopappus multicaulis var. *multicaulis.* MEXICO: Coahuila, 0.5 mi. S Nava, on Hwy. 57, Northington 233. TEXAS: Atascosa Co., 11 mi. S Pleasanton on US 281, Northington, Bierner, and Tomb 215; Bell Co., 23rd St. and West Ave. H in Temple, Northington 35; Caldwell Co., Luling at East Pierce and South Pine Streets, Northington 7; Dewitt Co., US 183 in Cuero, ½ blk. off Morgan Street, Northington 155; Duval Co., 6 mi. N Freer on Tex. 16, Northington 138; Gonzales Co., St. Lawrence and Fair St., Northington 20; Hidalgo Co., US 281, 13.4 mi. N FM 490 jct. US 281, Northington, Bierner, and Tomb 213; Jim Hogg Co., Tex. 16, 5.5 mi. N Hebbronville, Northington 135; Jim Wells Co., US 281, 4 mi. S jct. FM 716 and US 281, Northington, Bierner, and Tomb 214; Liberty Co., Deevers, Northington and Bierner 158; McMullen Co., Tex. 16, 2 mi. N Tilden, Northington 141; Medina Co., Devine, Wilson Drive and Hondo Ave., Northington 13; *San Patricio Co., 15 mi. SE Sinton on Hwy. 181, Northington 151; San Patricio Co., Hwy 181, 15 mi. SE Sinton, Northington 152; Starr Co., FM 649, 11 mi. N El Sauz, Northington 117; Travis Co., US 71, 18 mi. W Bastrop, Northington 18; *Wilson Co., 1.8 mi. S Nixon on Hwy. 80, Northington 144-146; *Wilson Co., 2.1 mi. S Nixon on Hwy. 80, Northington 147; *Zapata Co., 6.3 mi. SE Arroyo Veleño, SE of Zapata on Tex. 83, Northington 120; Zapata Co., Hwy. 83, 6 mi. NW San Ignacio, Northington 123.

Pyrrhopappus multicaulis var. *geiseri.* OKLAHOMA: Garvin Co., US 177 S in Stratford, Northington 230; Murray Co., Hwy. 77 N Davis, Northington 42; Oklahoma Co., I-35, 1.6 mi. S I-44 turnpike entrance, Northington 226; Oklahoma Co., I-44, 2 mi. W Chandler interchange, Northington 227. TEXAS: Collin Co., Hwy. 75, 2 mi. N Plano, Northington 38; Cooke Co., I-35, 3 mi. N FM 922, Northington 218; Denton Co., Hwy. 77 at Sanger, Northington 40; Denton Co., I-35, 9 mi. S FM 922, Northington 217; Hill Co., I-35E, I-35E

and I-35W jct., Northington 37; Houston Co., Tex. 21, 3.1 mi. NE Trinity River, Northington and Bierner 202; McLennan Co., I-35, 24 mi. N Waco, Northington 36; McLennan Co., I-35, 1.9 mi. S FM 2837, Northington and Whiffin 271; Travis Co., I-35, 1 mi. N Pflugerville exit, Northington 34.

Pyrrhopappus rothrockii. MEXICO: Durango, Hwy. 40, 29 mi. S Durango, Northington 235; Durango, 36 mi. SW Guadalupe Victoria on Hwy. 40, Bierner and Whiffin 285; Jalisco, Hwy. 15, 5.4 mi. S Arenal, Northington 234. NEW MEXICO: Doña Ana Co., Hwy. 70 and 80 W Las Cruces, 0.2 mi. W Rio Grande River, Northington 244.

Pyrrhopappus grandiflorus. OKLAHOMA: Blaine Co., Hwy. 8N, Roman Nose State Park, Northington 48; Carter Co., I-35, 8 mi. S Ardmore, Northington 81; Cleveland Co., 3 mi. E US 77 SE Norman on Pauline's Patch Road, Northington 88; Ellis Co., 10 mi. N Canadian River on Okla. 283, Northington 50; Murray Co., Davis, Davis and 3rd streets, Northington 86; Pottawatomie Co., US 177, 4.9 mi. S jct. with 59E, Northington and Whiffin 279.

POPULATIONAL STUDIES

Bioecology.—The species of *Pyrrhopappus* are predominantly allopatric, their ranges apparently being partially determined by edaphic factors. The two perennial species, *P. grandiflorus* and *P. rothrockii*, are notable exceptions however. *P. grandiflorus*, a perennial with a well-developed tuber at the base of each tap root, occurs over a wide region of the south-central United States from Kansas to central Texas and grows in a variety of soil types including both clay and sand. *P. rothrockii*, which is endemic to the lower mountainous regions of Mexico, New Mexico, and Arizona, also tolerates a variety of soil types.

The species are basically mesic, being found primarily in areas of water accumulation, usually along roadsides, in ditches or in low, vacant, usually disturbed lots throughout most towns and cities. Although predominantly weedy, their occurrence in adjacent fields and pastures has not been especially noteworthy. In fact, *Pyrrhopappus* was not observed growing in heavily grazed fields or pastures. It is not known if the plants are grazed preferentially, but because they are always absent from grazed fields, it seems likely that they are at least edible and probably not distasteful to grazing animals.

Pyrrhopappus first appears with the early spring rains and warm weather, and its departure parallels the arrival of the yet greater heat and reduced rainfall, which is typical of early to midsummer in the regions concerned. However, heavy rain in the early autumn often results in a reappearance of the species, probably from that summer's seed crop in the case of the annual taxa and from the recurrent rootstocks of the perennials.

P. grandiflorus and *P. rothrockii* occur as infrequent, mostly small, populations of 20 to 50 or occasionally more numerous plants. Following abundant rain, larger populations can be seen for several miles along the roadside. However, at such times the frequency of plants does not approach the miles of blanketlike roadside coverage exhibited by the annual species. In exceptionally dry years, the perennial species are difficult to locate as populations, but the annual ones still exist as fairly large, although diminished, populations.

With the exceptions of *P. rothrockii*, and *P. grandiflorus*, both of which are capable of vegetative propagation, reproduction is completely sexual. Judged by

my own experiments and observations, the species of *Pyrrhopappus* are largley self-sterile. Judging from the large number of viable seeds set per head in the field, presumably the flowers are visited by numerous and efficient pollinators. Although a study of these vectors has not been made, at various times several different beetles, spiders, and bees have been observed on the heads, one of which species is the black bee, *Andrena verecunda.* According to Shinners (1958), this bee pollinates *Pyrrhopappus* exclusively and "in defiance of all the laws of busy bees, does nothing from high noon until after sunrise the next day."

All the taxa of *Pyrrhopappus* open their heads facing the east at sunrise and follow the movement of the sun until approximately noon when they close completely until the following morning. Each head opens from two to four days in succession, opening each morning with a new series of florets receptive to pollination. The actual time of closing varies with the degree of shade and moisture available, presumably as a result of a heat-dryness mechanism that causes the involucral bracts to close and the ligules to curl inward.

Plant variability and population structure.—The species of *Pyrrhopappus*, especially the annual ones, exhibit considerable morphological variability, both within and between populations. This is especially true of vegetative structure and plant habit, the latter apparently being affected by environmental variables such as soil, moisture, and temperature. For example, nearly all of the species have a tendency to become multicaulescent with age when growing in dry, hard, rocky soil; thus *P. carolinianus*, which is normally an erect plant with entire or single-lobed, lanceolate upper leaves and glabrous stems, has occasionally been observed with a much reduced plant height, increased multicaulescence, and increased lateral lobes on the upper leaves and some stem pubescence, either singly or in combinations of two or even three of these atypical features. Such individuals have been observed in Tennessee, Mississippi, and eastern Arkansas, all well removed from possible genetic contamination by other species possessing some or all of these morphological characters. In areas of sympatry, however, some of the variation is undoubtedly due to occasional gene exchange between taxa.

Leaf morphology, although usually consistent within a taxon and even more so within a single population of that taxon, can vary from lanceolate and entire to quite pinnatifid with three or four lateral lobes per leaf. Such extreme plasticity within a taxon is rare, but lesser degrees of it are fairly common and these have probably caused much of the taxonomic confusion in those treatments prepared from herbarium specimens alone. Variation in habit and leaf morphology is also affected by the maturity of plants. For instance, very young plants of *P. multicaulis* and *P. grandiflorus* all appear very similar in their above ground morphology, having a single, scapelike stem bearing a single head with a basal rosette of pinnatifid leaves. As they become mature, *P. grandiflorus* continues and enlarges this habit often adding one or two more stems. *P. multicaulis* var. *multicaulis* loses the single erect stem, but produces numerous others that are prostrate laterally for a few centimeters before ascending, and *P. multicaulis* var. *geiseri* remains erect, producing numerous secondary, lateral branches and cauline leaves

while often losing the basal rosettes. Thus, fragmentary collections of young plants not including the root structure are often very difficult, if not impossible to identify.

Natural hybridization between taxa of *Pyrrhopappus* further heightens the taxonomic difficulties. Although I have not been able to establish such hybridization experimentally, natural hybrids between the tetraploid, *P. grandiflorus*, and the diploid, *P. multicaulis* var. *geiseri* have been observed in the field, and, as indicated elsewhere (cytological section), their triploid condition and presumably largely F_1 status has been documented. Shinners (1958) also reported hybrids between *P. carolinianus* and *P. multicaulis* var. *geiseri* in northeast Texas. Field observations and cytological, chemical, and palynological data accumulated in this study all indicate natural hybridization, which, therefore, must be considered when discussing the morphological variability found in the genus.

Taxonomic problems.—Considering the above, resolution of many of the more pressing systematic problems can only come from extensive field observations and populational studies. One of the more complex taxonomic groups has been that of *P. multicaulis* var. *geiseri.* This taxon was first described as a species by Shinners (1951). More recently, it has been treated as a "suite of . . . introgressants" between *P. carolinianus* and *P. multicaulis* "owing to widespread genetic intercontamination" (Correll and Johnston, 1970). Experimental crossing studies should help resolve the controversy surrounding this taxon, but my own observations suggest that the populations concerned are recognizable geographic units showing strong affinity with *P. multicaulis* var. *multicaulis.*

If *P. multicaulis* var. *geiseri* is in fact merely a series of introgressant populations, then, based on the frequent and widespread distribution of these populations, a considerable amount of backcrossing with both parents should be expected. If such backcrossing with *P. carolinianus* exists, populations would regularly occur demonstrating a morphology composed of all combinations of the distinctive characters involved. Thus, throughout the area of sympatry between introgressant populations and those of *P. carolinianus*, populations should randomly occur exhibiting a range of morphological characters from pure *P. carolinianus* to that of the intermediate morphology of the putative introgressant forms.

Populations of *P. carolinianus* from Louisiana and Oklahoma were examined for stem pubescence, plant height, and number of pairs of lateral lobes on upper leaves. The same was done for populations of *P. multicaulis* var. *geiseri* in northeast and central Texas and Oklahoma. No sites were found in which the population structure even approached that of a backcross complex mentioned above, and as can be seen by Fig. 11, only rarely was there any morphological intermediacy expressed within a population. In general, then, the proposed introgressant populations appeared very consistent morphologically, both intra- and interpopulationally throughout the range of sympatry between *P. carolinianus* and *P. multicaulis* var. *geiseri.*

As a result of considerable field observations and detailed populational study, I conclude that present-day hybridization between *P. carolinianus* and *P. multicaulus* var. *geiseri* is not a significant factor in the morphological variation found

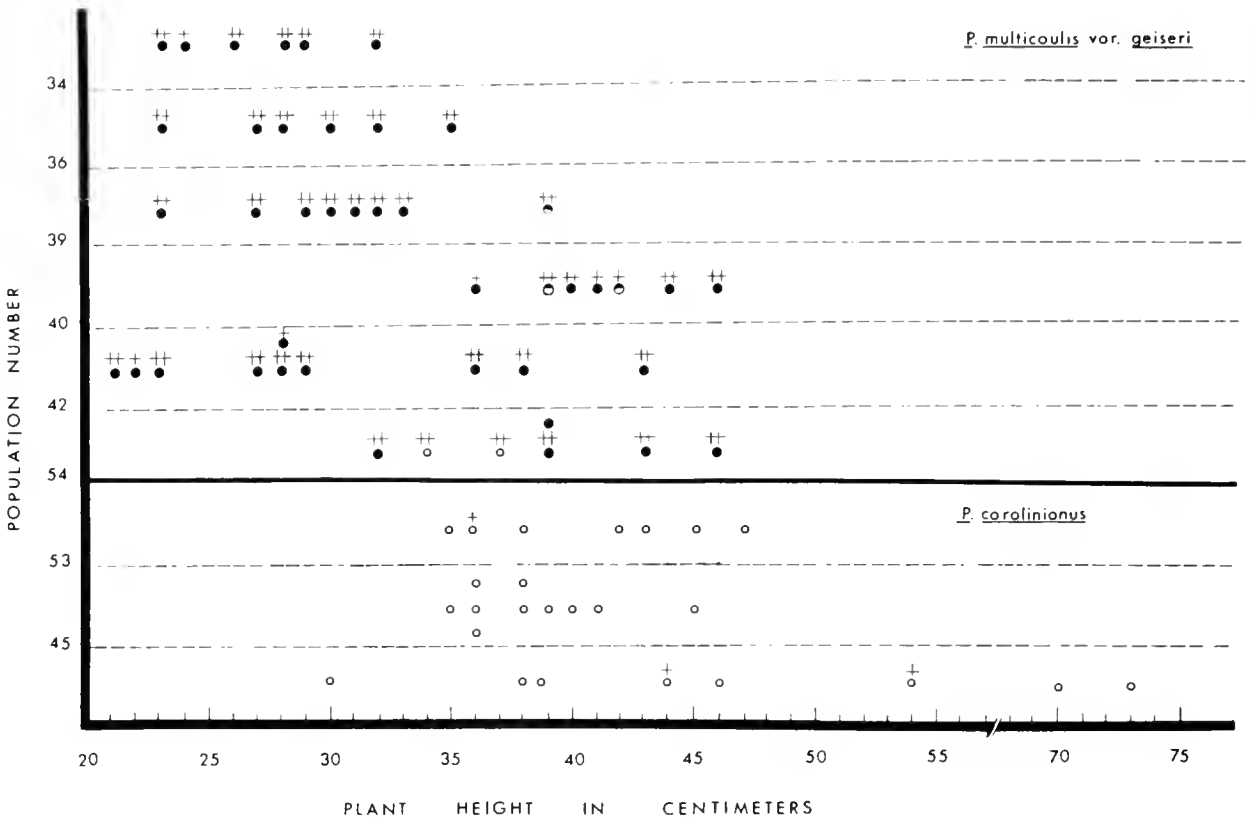


FIG. 11.—Graphic representation of three "pure" populations of *P. carolinianus* and six populations of *P. multicaulis* var. *geiseri* examined for three diagnostic morphological characters. Pubescence of lower stem: glabrous indicated by open circles; 1-10 trichomes per centimeter by half open circles; 11 + trichomes per centimeter by closed circles. Lateral lobe pairs: 0 or 1 indicated by circle only; 2 pairs by a plus above circle; and 3-5 pairs by a double plus. Sample 34 is from Travis Co., Texas; 36, McLennan Co., Texas; 37, Hill Co., Texas; 39, Collin Co., Texas; 40, Denton Co., Texas; 42, Murray Co., Texas; 45, Canadian Co., Oklahoma; 53, Calcasien Par., Louisiana; and 54, Acadia Par., Louisiana.

in the two taxa. Thus, I do not feel that the populations in question are the result of current introgressive hybridization.

In an attempt to resolve the taxonomic status and position of *P. multicaulis* var. *geiseri*, field observations and a populational morphological study were utilized. If *P. geiseri* were a valid species, clearly distinct from *P. multicaulis*, one would expect hybridization to produce highly variable populations showing a wide range of intermediate features, especially in the regions of sympatry. If on the other hand, the complex is a single species comprised of two intergrading regional varieties, a north-south clinal gradation in morphology would be expected.

The morphological characters used for this study are presented in Table 5; Fig. 12 shows graphically the populations examined. Briefly, these populations exhibit a clinal gradation in morphological characters from *P. multicaulis* var. *multicaulis* in south Texas to *P. m. var. geiseri* in north-central Texas and southern Oklahoma (see Fig. 13). In central Texas there is a zone of clinal transition that begins in the vicinity of the southern edge of the Edwards Plateau and concludes in north-central Texas. It is largely for these reasons that I treat the popu-

TABLE 5.—*Morphological characters differentiating between* P. multicaulis *var.* multicaulis *and* P. multicaulis *var.* geiseri.

Pyrrhopappus multicaulis var. *multicaulis*	*Pyrrhopappus multicaulis* var. *geiseri*
1. Stems 5 or more, from the root crown, at first more or less prostrate but soon ascending.	1. Stems usually 1, erect (occasionally 2 or 3 developing with age).
2. Plant at maturity 15 to 40 cm high.	2. Plant at maturity 35 to 65 cm high.
3. Lateral branches usually 3 per stem.	3. Lateral branches usually 3-15 per stem.

The variability of characters 1 and 2 among selected individuals and populations are shown by scatter diagrams in Fig. 12. The variation in character 3 is expressed for each plant as a ratio of branches per stem. For this study, eight populations of ten plants each were sampled from north to south Texas as shown in Fig. 13. These populations are represented by letters A-H, north to south consecutively.

lations concerned as regional varieties of *P. multicaulis*: var. *multicaulis* and var. *geiseri.*

In addition to the populational problems discussed above, recent field work in south Texas has shown the existence of an interesting series of populational varieties of *P. multicaulis*, in which one finds cream-colored heads with greatly reduced ligules, differing significantly from those typical of this species. These populations occur predominantly in the Coastal Plains, but have been encountered occasionally in more inland sites within the range of *P. multicaulis.* Although the existence of the occasional cream-colored form has been recognized in the genus for some time (Harper, 1933), there have never been other morphological differences reported in connection with this, nor have they been considered as populational. I have observed from time to time cream-colored heads among otherwise normal populations in all of the annual species of *Pyrrhopappus.* In such populations, fewer than one plant in a thousand has a cream-colored head, according to my estimates.

Along the coast of Texas in San Patricio and Refugio counties, however, populations have been examined with as many as 85 to 95 per cent of the plants possessing cream-colored heads. However, the percentage of these plants that also have reduced ligule size and often modified plant habit varies in these populations from as high as about 60 per cent to as low as about 10 per cent. In short, populations may be found that vary from nearly typical *P. multicaulis* having normal-sized, yellow ligules through intermediate populations with varying populations of normal-sized, cream-colored ligues to normal-sized, yellow ligules to very reduced, cream-colored ligules. Almost every possible combination of ligule size and color variation was observed in varying degrees in the populations with one exception: plants with heads having reduced ligules were invariably cream-colored.

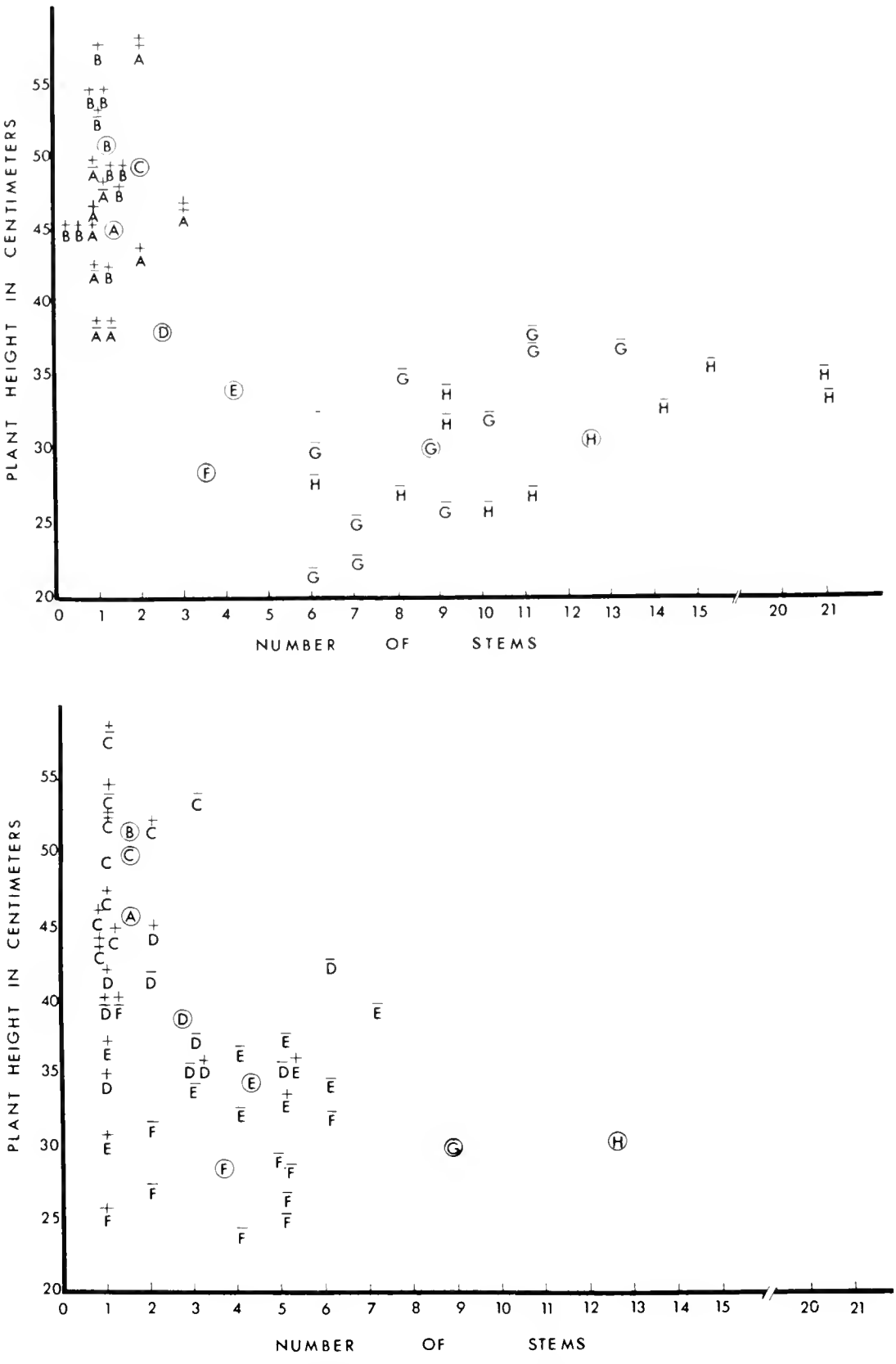


FIG. 12.—Scatter diagrams showing the clinal gradation between *P. multicaulis* var. *multicaulis* and var. *geiseri*. The three characters expressed are plant height (X axis), number of main stems (Y axis), and the ratio of number of branches per stem: 0:1 to 2.5:1 indicated by a minus sign; 2.6:1 to 5.0:1, by a single plus; 5.1:1 to 8.0:1, by a plus above a minus; and 8.1:1 to 15:1, by two plus signs, one above the other. Each letter represents an individual plant from the indicated population (see Fig. 13 for population localities as expressed by letters). The circled letter represents the population average for the first two characters (X and Y axes).

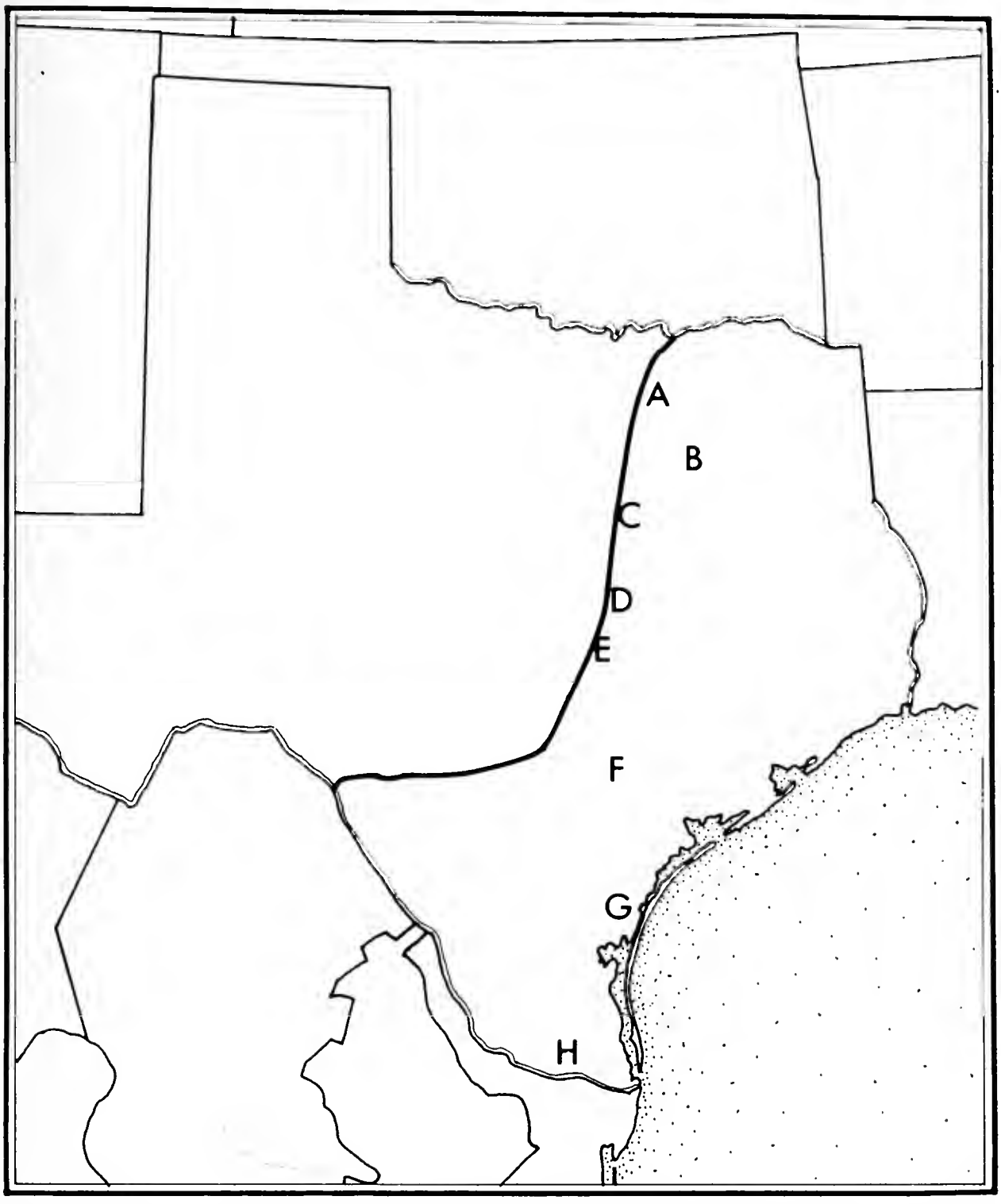


FIG. 13.—Texas localities for population samples of *Pyrrhopappus multicaulis* examined morphologically: A, Collin Co.; B, Kaufman Co.; C, Hill Co.; D, Bell Co.; E, Williamson Co.; F, Gonzales Co.; G, San Patricio Co.; H, Hidalgo Co. The solid line running through the state represents the approximate position of the eastern edge of the Edwards Plateau.

Farther inland, the two morphologically extreme forms, *P. multicaulis* and the cream-colored plants of reduced ligule size, become more predominant with few morphologically intermediate individuals. In fact, two populations in Zapata and Hidalgo counties consisted of only the two existing populational types. From these observations, it is difficult to account for such varying populational struc-

ture, but it would seem that very few gene differences are involved. Although reduced, cream-colored forms have only been observed in populations containing normal *P. multicaulis*, such forms might also occur in other species. Because the small, cream-colored heads are inconspicuous, it cannot be said with certainty that such forms occur only with or in populations of *P. multicaulis*. Chemical and preliminary morphological studies, however, suggest that the plants with reduced, cream-colored ligules are probably worthy of at least varietal rank, but because of the complex populational structure and the clear need for further study, nomenclatural status has not been determined.

Pyrrhopappus carolinianus and *P. georgianus* occur primarily in northern Florida, Georgia, and South Carolina where they are sympatric. *P. georgianus* was described by Shinners (1953), but subsequently was reduced to a variety of *P. carolinianus* by Ahles (1964). Examination of herbarium materials failed to indicate a clinal problem with *P. georgianus* and *P. carolinianus* as was found with *P. multicaulis* and *P. geiseri*. Indeed, field work in the area of sympatry suggested that two distinct taxa occurred in this region. In addition, flavonoid studies have shown a consistent difference between these taxa that correlates well with the morphological features that distinguish them.

Although flavonoid data can be considered suggestive only, and some natural hybridization may be occurring, I do not feel, from the preliminary examinations mentioned above, that these two taxa deserve an extensive populational examination. In fact the taxa concerned seemed distinct both ecologically and morphologically, and, when found growing in proximity, evidenced little, if any, gene exchange. They are thus considered distinct species.

Generic Relationships and Phylogeny

Generic relationships.—Pyrrhopappus is a member of the tribe Cichorieae, which has long been considered the most natural and recognizable of the subdivisions of the family Compositae. Within the tribe, however, generic alignment has varied considerably with each treatment. According to Stebbins (1953), the author of the most recent reorganization of the tribe, all the early treatments were highly artificial due to the fact that although other morphological characters such as pollen, achene, receptacular paleae, and anther appendage characteristics were available and used to some extent in varying combinations and with varying emphasis, the greatest emphasis was placed on pappus characteristics. While still one of the more important characters, its diagnostic use was not without misinterpretation. For instance, the absence of pappus in two taxa does not necessarily indicate a close relationship. In addition to the above characters, the availability of chromosome numbers and morphology, which was spawned by relatively recent advances in cytological techniques, enabled Stebbins to incorporate many new data into his study. As a result, Stebbins placed *Pyrrhopappus* in the subtribe Microseridinae along with the genera *Microseris*, *Phalacroseris*, *Apargidium*, *Agoseris*, *Krigia*, and *Picrosia*. In so doing, he stated:

> The recognition of this subtribe is based primarily on the fact that the first four genera mentioned [*Microseris*, *Phalacroseris*, *Apargidium*, and *Agoseris*] are closely similar in

general habit of growth, geographic distribution and chromosomes, and are connected by transitional species.

Pyrrhopappus, *Krigia*, and *Picrosia* are included in the same subtribe with the above four genera because of similar pubescence, stigma, and pollen characters. These seven genera are placed together despite the fact that the first four genera mentioned all have base chromosome numbers of $x=9$, whereas *Pyrrhopappus* and *Krigia* have $x=6$ and $x=5$, respectively; the number is unknown for *Picrosia*. In addition, *Krigia* and *Pyrrhopappus* have eastern North American distributions and *Picrosia* is endemic to South America, whereas the four genera having $x=9$ chromosomes all have western North American distributions.

Previous authors of major systems, such as De Candolle (1838), Gray (1888), Bentham and Hooker (1873), and Torrey and Gray (1843), placed *Pyrrhopappus* close to or near *Taraxacum*, *Chondrilla*, *Lactuca*, and *Calycoseris*, none of which is included in the Microseridinae by Stebbins (1953). Stebbins presumably used chromosome number and distribution as his primary criteria for not including any of these genera in the same subtribe with *Pyrrhopappus*, as only *Calycoseris* is native to North American and none has the base chromosome number of $x=6$.

Although my study has not been sufficiently extensive to establish with any degree of certainty those genera most closely related to *Pyrrhopappus*, some tentative conclusions concerning such relationships may be inferred. As for Stebbins' treatment, he selected as the most closely related genus to *Pyrrhopappus* the monotypic, South American genus, *Picrosia*, which he thought to be "probably a specialized offshoot of *Pyrrhopappus*." Although *Picrosia* is very similar to *Pyrrhopappus* in many morphological features, in the absence of cytological and chemical data a strong relationship between the two genera cannot be firmly established. In addition to *Picrosia*, *Krigia* shares many diagnostic features with *Pyrrhopappus*, including distribution. *Lygodesmia*, placed by Stebbins in the subtribe Stephanomerinae, also must be considered. In fact *Lygodesmia* appears to be more closely related to *Pyrrhopappus* than do the four previously mentioned genera in the Microseridinae with base chromosome numbers of $x=9$. *Lygodesmia* is similar to *Pyrrhopappus* in pollen, habit, chromosome number (it is dibasic with $x=9$ and 6), and form of involucral bracts and pappus. Because of this apparent closer relationship of *Pyrrhopappus* to a member of another subtribe than to the principal members of the subtribe in which it has been placed, I feel that some realignment may be called for when sufficient data become available.

Phylogeny.—The establishment of a phylogenetic scheme for a small, closely knit genus such as *Pyrrhopappus* is made difficult by the absence of a great number of diagnostic morphological characters and by the presence of a high degree of cytological uniformity among the taxa. However, such an evolutionary interpretation can be made based on a combination of morphological, chromosomal, and chemical characters, particularly as these relate to distributional patterns.

The initial step in the assessment of the evolutionary trends in *Pyrrhopappus* is the evaluation of the various taxa for primitive and derived (advanced) fea-

TABLE 6.—*Some of the characters considered primitive and derived for* Pyrrhopappus.

Primitive	Derived
1. diploid chromosome number	1. tetraploid chromosome number
2. annual habit	2. perennial habit
3. basal leaf rosette absent	3. basal leaf rosette present
4. leaves entire	4. leaves pinnatifid
5. mesophytic	5. xerophytic
6. stems leafy	6. stem leaves reduced

tures. The assignment of "primitive" or "derived" to a given character generally follows accepted trends. For example, a basal leaf rosette is considered as derived from cauline leaves with definite internodes, and increased ploidy levels in chromosome number is usually thought to be derived. Certainly, such generalities depend on the standard, circular argument that primitive characters are those characters possessed by primitive taxa and the reverse for advanced characters, thus a familiarity with the taxon in question is a necessary consideration (see Table 6).

Occasionally, such character assignments are reversible within the genus as is the case with several species of *Pyrrhopappus*. Thus, *P. rothrockii*, although thought to be derived, tends to have entire leaves.

With such difficulties taken into consideration, the primitive or derived relationships between the taxa can be reasonably suggested. In an effort to express these relationships numerically, I have incorporated the Wagner Divergence Index (Wagner, 1961, 1966) whereby a numerical value of 0.0, 0.5, or 1.0 is assigned each of the above character states depending on their presumed primitive, intermediate, or derived conditions. The sum of such values expresses the degree of advancement from the theoretically primitive state for each taxon

TABLE 7.—*Divergence index values of the species of* Pyrrhopappus.

	P. carolinianus	*P. multicaulis* var. *geiseri*	*P. multicaulis* var. *multicaulis*	*P. georgianus*	*P. rothrockii*	*P. grandiflorus*
Chromosone number	0.0	0.0	0.0	0.0	0.0	1.0
Root	0.0	0.0	0.0	0.0	1.0	1.0
Basal leaf rosette	0.0	0.5	1.0	1.0	1.0	1.0
Leaf margin	0.0	1.0	1.0	1.0	0.0	1.0
Meso- or xerophytic	0.0	0.5	0.5	0.5	1.0	0.5
Stem leaves	0.0	0.0	0.5	1.0	1.0	1.0
Totals	0.0	2.0	3.0	3.5	4.0	5.5

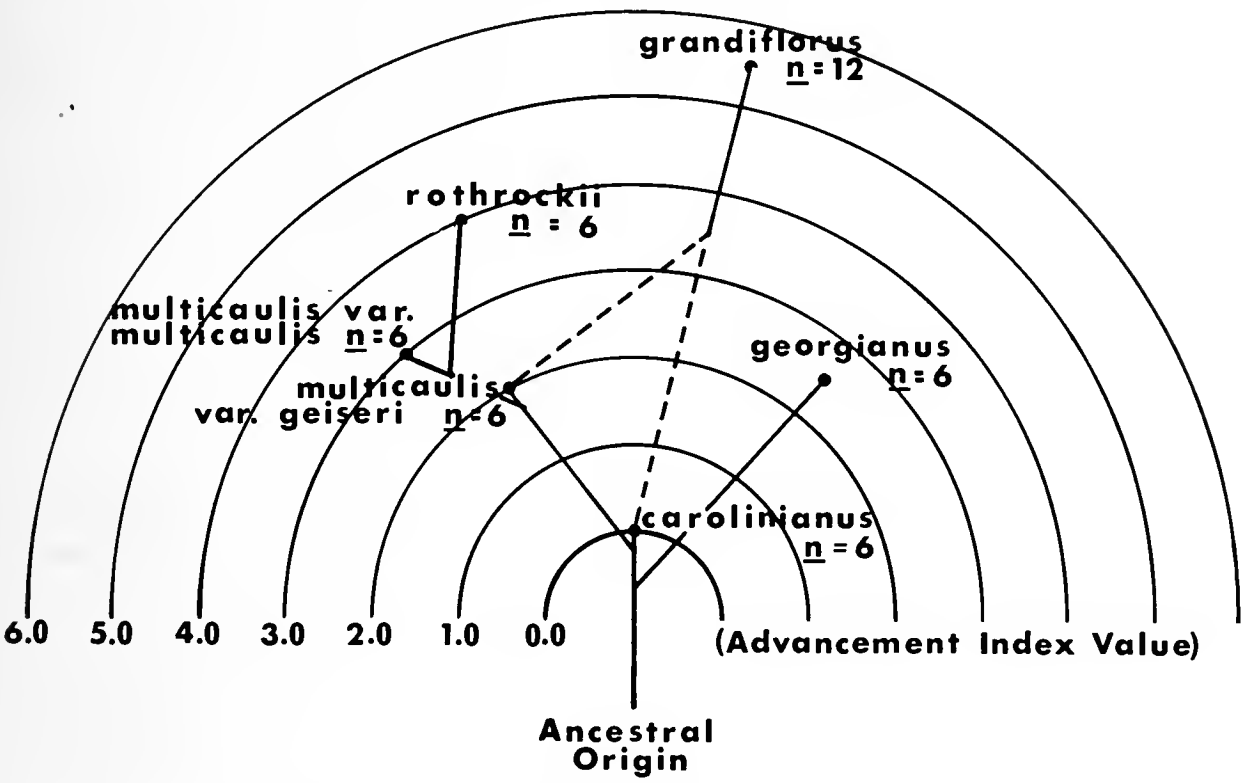


FIG. 14.—Diagram of species relationships and degree of advancement in *Pyrrhopappus*. The base of each line indicates the origin of each taxon. The dotted lines to *P. grandiflorus* indicate its possible allotetraploid origin from the two indicated, extant taxa, or more probably from ancestral progenitors of one or both.

(Table 7). When the geographical distribution is then considered in light of these relative advancement values, a plausible phylogeny for the genus can be erected.

In such a phylogenetic scheme, the taxon having the greatest number of primitive characters is *Pyrrhopappus carolinianus* followed by *P. multicaulis* var. *geiseri* and *P. multicaulis* var. *multicaulis*. Based on the assignment of *P. carolinianus* as the most primitive species, the probable origin of *Pyrrhopappus* is believed to have been during the Mesozoic in the Appalachian refugium from which the genus spread south and west into available mesic grasslands. This migration southwestward resulted in increased adaptability to the more xeric conditions of the southwestern United States and Mexico as expressed by the most derived taxa, *P. rothrockii* and *P. grandiflorus*. The former taxon is a rhizometous perennial occurring at the southern and western limits of the generic distribution whereas the latter (a tetraploid) is a tuberous-rooted perennial occurring at the northwestern limits of the generic distribution. See Fig. 14 for a proposed relationship between the taxa of *Pyrrhopappus*.

SUMMARY

Cytological, palynological, chemical, and populational studies were carried out on *Pyrrhopappus*, a genus occurring throughout the southeastern and southwestern United States and Mexico. Six taxa were recognized as a result of this study, five species and one variety, including one new combination.

Cytotaxonomic work resulted in more than 100 meiotic chromosome counts for the genus with previously unreported counts for three of the taxa (Grashoff *et al.*, 1972). All but one of the taxa are diploid, $n=6$; *Pyrrhopappus grandiflorus* is tetraploid, $n=12$. Karyotypes for two of the diploid taxa were also established. Natural hybrids between the tetraploid and one of the diploid species resulted in populations containing $2n=18$, triploid individuals. Cytological work was useful in the treatment of the tetraploid species, *P. grandiflorus*, and helped lead to an hypothesis of a putative allotetraploid origin for that taxon.

Palynological studies established the external pollen morphology in *Pyrrhopappus* and revealed larger pollen with the occurrence of tetracolporate grains for *P. grandiflorus*.

Chemosystematic work led to the isolation and identification of flavonoid compounds in all taxa of the genus. Each identified compound was a flavone having the base structure of either apigenin or luteolin. These data were useful in the delimitation of taxa in that consistent differences in compound occurrence were found in most of the taxa. These differences closely paralleled morphological trends, especially in populational studies of *P. multicaulis* var. *multicaulis* and var. *geiseri*. Of special interest was the presence of anthochlor pigments in the ligules, this being the first report of their occurrence in the Cichorieae.

Morphological studies of natural populations were instrumental in the reduction of *Pyrrhopappus geiseri* to a variety of *P. multicaulis*. Similar field observations helped establish *P. carolinianus* and *P. multicaulis* var. *geiseri* as distinct from each other.

The cumulative cytological, palynological, chemical, and morphological data in conjunction with ecological and distributional observations made possible the construction of a plausible phylogeny for the genus. Thus, *Pyrrhopappus carolinianus* is considered most primitive, having as its probable origin the Appalachian refugium during the Mesozoic. The most derived taxa are the two perennial species at the western limits of the generic distribution, *P. rothrockii* and *P. grandiflorus*.

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