TAXONOMY OF THE GENUS *HELIOPSIS* (COMPOSITAE)[1]

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The genus *Heliopsis* is a member of the tribe Heliantheae of the family Compositae. It is represented by thirteen species, all of which are restricted to the western hemisphere. Although some of the species, particularly those of the United States, have received attention recently, there has been a great deal of confusion with regard to the status of several taxa. This confusion, in part, has been due to the lack of study of the genus throughout its entire range.

The genus is separated from other genera of the tribe in possessing fertile disk flowers, as well as fertile, persistent ray flowers, with marcescent ligules, achenes void of a pappus, or pappus of a slight crown of one or two short chaffy awns.

In order to gain information concerning relationships the problem was attacked in three ways: by a study of herbarium specimens,[2] by studying as many collections as possible in the research garden, and by studying populations in nature. These techniques involved conducting a hybridization program, cytological study, and an investigation of the ecological conditions throughout the range of the species.

History

In 1753, Linnaeus described species now referred to *Heliopsis* under the following three genera: *Buphthalamum*, *Silphium*, and *Rudbeckia*. *Buphthalamum helianthoides* was described from material collected in Pennsylvania, North Carolina, and Virginia, whereas *Silphium solidaginoides* and *Rudbeckia oppositifolia* were described from material from Virginia. These errors persisted until 1807 when Persoon described the genus *Heliopsis* and placed the three Linnaean species in synonomy. However, Persoon did not retain the earliest specific epithet employed by Linnaeus. Instead, he named the smooth-leaved taxon *Heliopsis laevis*. In 1826, R. Sweet recognized that *Buphthalamum helianthoides* L. and *Heliopsis laevis* Pers. were the same taxon. Consequently, he restored the Linnaean epithet of *helianthoides* in the publication, "Hortus Britannicus." Sweet's treatment unfortunately, was not generally known to the authors of American Floras until the late 1800's, thus the specific epithet employed by Persoon persisted for some time for the widely distributed *H. helianthoides* (L.) Sweet.

In his account of *Heliopsis* for the "Prodromus" of DeCandolle, (1836), Cassini treated the genus in three sections and recognized six species, two of which had been proposed by Hooker (1835) in "Companion to the Botanical Magazine." The sections were separated on the basis of achene characteristics and the number of series of involucral bracts.

In 1835, Rafinesque described the genus *Heliopsis*, as then known, under the generic name of *Helepta*. Three species, *H. grandifolia*, from the Carolinas, *H. parviflora* and *H. augustifolia* from eastern Kentucky, were included in this genus. The species were seperated on the basis of leaf shape and achene characteristics.

Torrey and Gray in "Flora of North America" (1842) accepted *H. laevis* Pers. as the only valid species and reduced *H. scabra* Dun. and *H. gracilis* Nutt. to varieties. Gray's later treatment of the North American flora (1878), reinstated

[1]Publication 606, Department of Botany and Plant Pathology, The Ohio State University.

[2]In order to conserve space, citation of specimens has been eliminated. A duplicated list of specimens examined and cited for this study is being sent to the major herbaria of the United States. The reader is also referred to the microfilm reproduction of the author's Ph.D. thesis on file at the University of Michigan library.

H. scabra and *H. gracilis* as species and added *H. parvifolia*, a newly described taxon from the southwestern United States and northern Mexico. In addition to the four taxa in the United States, he included a Mexican species, *H. buphthalmoides* Dun.

In 1797, Jacques described *Heliopsis buphthalmoides* under the genus *Anthemis*. From his description it is difficult to determine his reasons for this, except that in *Anthemis*, the rays may be fertile or neutral, and may be yellow, but are more often white. The type specimen has not been examined, but in *Anthemis* the leaves are alternate and pinnately dissected, a condition which never exists in *Heliopsis*. In 1819, Dunal transferred the species to *Heliopsis*, but failed to give Jacques credit for the specific epithet.

M. L. Fernald (1937) described *H. helianthoides* var. *solidaginoides* from herbarium material of this country as well as from the British Museum and the Linnaean Herbarium. He concluded that *Silphium solidaginoides* L. was a southern form of *H. helianthoides* (L) Sweet.

A Summary of the Chronological History of the Genus:

1. Linnaeus, C. (1753) Sp. Pl. Stockholm. 2: 904.
2. Jacques, N. J. (1797) Hart. Schoenb. 2: 13.
3. Persoon, C. H. (1807) Syn. 2: 474.
4. Dunal (1819) Mem. Mus. Paris 5: 56.
5. Cassini, H. (1822) Dict. Sc. Nat. 24: 327.
6. Rafinesque, C. S. (1825) Neogynt. 3: 231.
7. Sweet, R. (1826) Hort. Brit. 487.
8. Hooker, J. D. (1835) Comp. Bot. Mag. 1: 98.
9. De Candolle, A. (1836) Prodr. 5: 551.
10. Torrey, J. & Gray, A. (1842) Fl. No. Amer. 2: 303.
11. Gray, A. (1878) Syn. Fl. No. Amer. 2: 254.
12. Fernald, M. L. (1937) Rhodora 39: 456.

General Morphology

Caudex and roots.—The species of *Heliopsis* are herbaceous and perennial with the exception of four annual species, which are endemic to Mexico.

The persisting structure of the perennials is a woody caudex with a mass of branched and unbranched fleshy roots. Growth in the spring is from lateral buds along the underground rhizome. The root system varies with the environmental conditions in which the plant grows. In the more moist mesophytic habitats of the midwestern and eastern United States, southern Mexico and Central America, a fibrous root system prevails, but in the more xerophytic areas of the southwestern United States a modified tap root develops. Neither the caudex nor the root furnishes any feature of taxonomic value in distinguishing species; and the fact that these structures are seldom collected renders them valueless when dealing with herbarium material.

Stem.—The characters of the stem, especially the upper portions, afford some means of separating species. Rough, hispid or scabrous pubescence is an important distinguishing character in the species of the United States. Other species are pilose, hirsute or villous. The indumentum is generally confined to the upper stems or lateral branches and leaves.

Leaves.—The leaves, which are always opposite, afford good criteria in separating species. Four taxa, *H. brachactis*, *H. parvifolia*, *H. rubra*, and *H. helianthoides* ssp. *occidentalis* exhibit a deltoid, or deltoid-ovate type of leaf shape (fig. 1). In *H. filifolia*, the leaf is filiform. In other species the leaf shape is lanceolate, ovate or ovate-lanceolate.

The petiole length is a valuable character in separating *H. helianthoides* ssp. *occidentalis* from *H. helianthoides* ssp. *helianthoides*, the petiole of the latter always

being 1.5 cm. or longer, and that of the former seldom attaining 1.5 cm. and more often being nearly sessile.

The leaf margins are most often irregularly dentate, but occasionally, in some species, they are nearly entire or merely irregularly crenulate. The texture is mostly leathery and quite firm, but in the annual species it is usually thin and papery.

Involucre.—The phyllaries are of little value in separating taxa since they are highly variable within a given species in regard to shape, size, and pubescence. The species of the United States usually possess foliaceous outer phyllaries, whereas the species of Mexico and South America possess phyllaries which are only occasionally foliar.

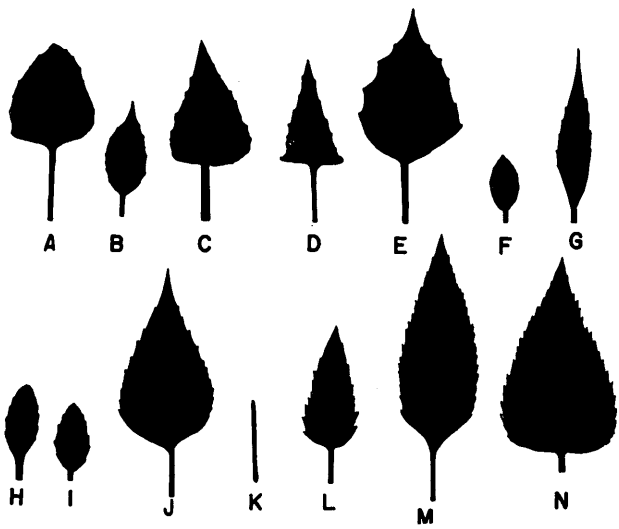

FIGURE 1. Leaf outline drawing of species of *Heliopsis*. **A.** *H. annua*; **B.** *H. parviceps*; **C.** *H. brachactis*; **D.** *H. parvifolia*; **E.** *H. rubra*; **F.** *H. procumbens*; **G.** *H. lanceolata*; **H.** *H. decumbens*; **I.** *H. longipes*; **J.** *H. buphthalmoides*; **K.** *H. filifolia*; **L.** *H. gracilis*; **M.** *H. helianthoides* ssp. *helianthoides*; **N.** *H. helianthoides* ssp. *occidentalis*. Reduced ¾ natural size).

Receptacle and palea.—The receptacle is broadly convex and hollow, although only inconspicuously so in *H. helianthoides*. The pales are lanceolate, acute, conduplicate, becoming stiff and persistent after maturity. The color of the apex is red, purple or yellowish-brown, and offers ready means of separating certain taxa.

Corollas.—The heads are heterogamous with styliferous, fertile ray flowers and perfect, fertile tubular disk flowers. The corollas of both the ray and disk flowers are yellow in all taxa except *H. brachactis* and *H. parviceps*, in which they are deep purple.

Pappus.—The genus is characterized by the absence of the pappus, although occasionally in the taxa of the United States, especially *H. helianthoides* ssp. *scabra*, the pappus is rarely represented by 2–3 chaffy awns or a crenulate ridge.

Geographic Distribution of the Genus

The known areas of distribution of *Heliopsis* are shown on the maps which accompany the taxonomic treatment. In general, herbarium material of the North American taxa has been ample to plot distributions with a great deal of

accuracy, but there are still some large disjunctions, particularly in the southern and southwestern areas of the United States and Mexico. Herbarium material examined from Central and South America is insufficient to plot accurate distributions of all taxa. In some instances only the holotype has been available for study. In others, the distribution seems to be disjunct for several reasons. As mentioned above, it may be due to the incompleteness of collections. On the other hand, the species may be rare and consequently seldom collected.

The plants included in this study occur in southern Canada, United States, Mexico, Central America and South America. In Canada, *Heliopsis* occurs only in the southern portions of Quebec, and westward to southeastern Saskatchewan. In the United States, the genus is widespread, ranging from Maine westward to North Dakota, southward through the Great Plains to New Mexico and eastward through eastern Texas to northern Florida.

From southeastern Arizona and southwestern Texas the genus ranges southward through Mexico, Central America and into South America to central Bolivia.

TABLE 1

Tabular arrangement of material which furnished cytological counts (In all, n=14)

H. helianthoides ssp. *helianthoides*	
Tippecanoe Co., Indiana	D. M. Smith *s.n.*
Monroe Co., Indiana	T. R. Fisher 533
Crawford Co., Indiana	C. B. Heiser, Jr. 3275
Cattaraugus Co., New York	C. B. Heiser, Jr. s.n.
Botetourt Co., Virginia	W. P. Stoutemire s.n.
Richland Co., Ohio	R. W. Long 528
H. helianthoides ssp. *occidentalis*	
Depage Co., Illinois	F. Swink s.n.
St. Louis Co., Minnesota	*O. Lakela s.n.
St. Croix Co., Wisconsin	C. B. Heiser, Jr. 3253
H. helianthoides ssp. *scabra*	
Shannon Co., Missouri	C. B. Heiser, Jr. (seedling transplant)
Franklin Co., Missouri	T. R. Fisher 410
Reynolds Co., Missouri	C. B. Heiser, Jr. (seedling transplant)
H. parvifolia	
U. S. D. A., Beltsville, Maryland**	
H. annua	
Guanajuata, Mexico	*L. A. Kenoyer 2412
H. rubra	
near Puerto Escondido, Baja California, Mexico	*A. Carter 2866

* Seed obtained from herbarium specimens.
** Exact location of source material unknown.

Cytology

Cooper and Mahony (1935) reported a chromosome number of n=16 in *H. helianthoides*. This number has never been found in this species or any other species examined during the course of this investigation. Instead, a chromosome number of n=14 has been found in *H. helianthoides* as well as in *H. annua*, *H. parvifolia* and *H. rubra*. In *H. helianthoides*, several collections from the midwestern and eastern United States were examined (table 1, fig. 2).

Meiotic division figures were regular in all material studied. Microsporocytes were smeared using the acetocarmine smear technique after preliminary fixation in 3:1 acetic acid-alcohol. Specimens from all available collections of taxa

which provided material for counts have been deposited in the herbarium of Indiana University.

Hybridization Experiments

This taxonomic study was conducted using the *H. helianthoides* complex, *H. parvifolia*, *H. rubra*, and *H. annua*. The parental plants for these experiments were obtained from seed or by clone transplant. In the case of *H. annua* and *H. rubra*, the fruits were obtained from herbarium material of recent collections.

All taxa used in this study are self-incompatible for all practical purposes since only rarely did any seed set occur in self-compatibility tests. Thus, crossing races of plants was comparatively easy since emasculation was unnecessary. The immature heads were bagged before the ray flowers appeared. Pollen was transferred until all stigmas of the plant which was being used as the egg plant had withered. In this manner, seed-set percentages could be determined.

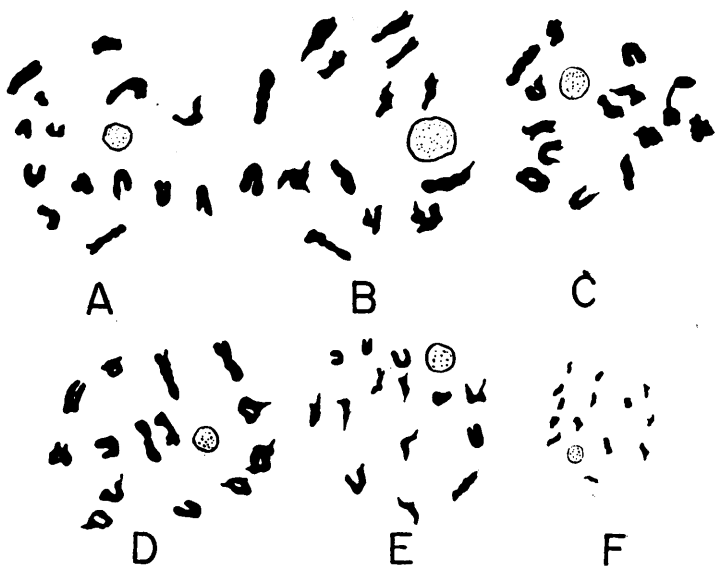

FIGURE 2. Camera lucida drawings of representative meiotic chromosome complements from pollen mother cells. (X, 1300)

A. *H. helianthoides* (L.) Sweet ssp. *helianthoides*, Monroe Co., Indiana, *Fisher 533*.
B. *H. helianthoides* (L.) Sweet ssp. *occidentalis*, St. Louis Co., Minnesota, *O. Lakela s.n.*
C. *H. helianthoides* (L.) Sweet ssp. *scabra*, Franklin Co., Missouri, *Fisher 410*.
D. *H. parvifolia* Gray, U. S. D. A., source unknown.
E. *H. rubra* Fisher, Baja California, Mexico, *Carter 2866*.
F. *H. annua* Hemsl., Guanajuata, Mexico, *L. A. Kenoyer 2412*.

As soon as the stigmas of all the disk flowers had withered, the heads were covered with cheese-cloth and tied securely an inch below the involucral bracts. These plants were left in the field until after the first frost, after which they were collected and stored in a cool, dry room.

Hybridization within the *H. helianthoides* complex was easily accomplished while interspecific crosses were made with greater difficulty (fig. 3). In the latter, the stigmas would persist, apparently indicating that the previously applied pollen did not effect fertilization. Therefore, interspecific crosses required repeated

pollinations over a longer period of time than intraspecific crosses, to insure any seed set.

Pollen viability was determined by using cotton blue in lactophenol. Those pollen grains which took a deep blue stain were counted as "good" or viable.

Interspecific Crosses

H. helianthoides *ssp.* occidentalis *X* H. parvifolia.—Only with difficulty was this cross possible and then only by repeated pollinations over a period of 10 to 14 days. Nine separate crosses, including reciprocals, were attempted during the growing season. Fertilization was effected only when *H. parvifolia* was used as the egg parent and then only 3 to 5 percent seed set was obtained. Five hybrid seedlings grew to maturity, two of which were dwarfed plants and attained a height of only 18 inches. The other plants were intermediate between the parents in most characters (table 2). The leaf base angle[3] remained the same as in *H. parvifolia.* Pollen stainability was reduced from 96 percent in either parent to 34 percent in the hybrid. Fourteen bivalents were regularly present at metaphase I.

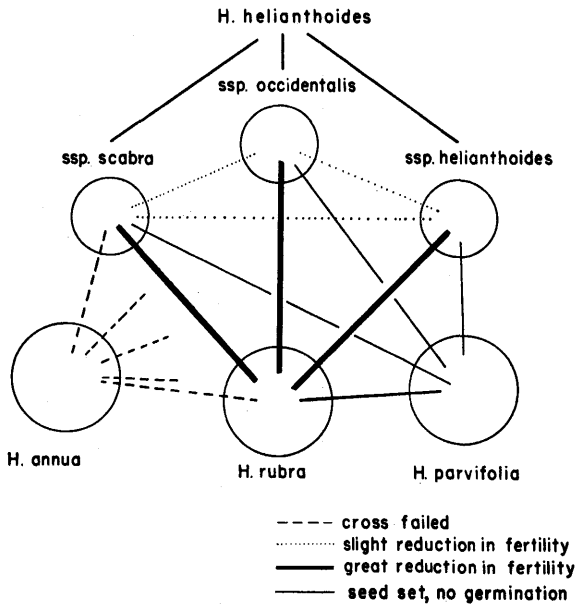

FIGURE 3. Crossing polygon showing the interfertility relationships among those *Heliopsis* species used in the artificial crosses.

The dwarfed plants produced many lateral branches just above the ground level, exhibiting a growth form resembling a ball or globe. Each of the lateral branches produced many heads, which suggested the use of the plant as a possible garden ornamental. Pollen stainability was essentially the same as in the other hybrids.

These dwarfed plants were left in the field during the following winter and, like one of the parents, *H. parvifolia,* failed to survive. An attempt was made to backcross the dwarfed hybrid with the parents. The only successful cross was

[3]The leaf base angle was computed with a protractor by measuring the angle formed by the base of the blade and the petiole.

with *H. helianthoides* ssp. *occidentalis* as the egg parent. This yielded only two plants which morphologically resembled the egg parent more closely than the pollen parent. Pollen stainability was approximately 35 percent, no appreciable increase in viability.

In the above crosses of *H. parvifolia* with *H. helianthoides* ssp. *occidentalis*, which involved great differences in leaf shape, the deltoid-lanceolate leaf found in *H. parvifolia* appears dominant. Long peduncle also appears dominant over short peduncle, and narrow leaf over broad leaf. Other characters are intermediate between the two parents suggesting that they are the result of multiple factors

TABLE 2

*Comparison of 9 characters in the parents and F_1 hybrids from inter- and intraspecific crosses in in the research garden (Leaf base, angle in degrees, pubescence scored 0-glabrous to 4-dense scabrous, all other measurements in centimeters).**

Cross	Leaf base angle	Petiole length	Pubescence	Peduncle length	Leaf length	Leaf width	Ray length	Ray width	Head width	Pollen stainability
H. hel. ssp. *occidentalis* (H-3)	102	1.2	4	32.4	12.5	6.8	3.6	1.0	2.8	96%
H. parvifolia (H-4)	135	3.0	2	29.5	8.8	2.5	2.4	1.1	1.3	96%
Hybrid (3x4)	135	2.5	2	29.3	9.0	3.9	2.5	1.0	1.5	34%
H. hel. ssp. *scabra* (H-8)	125	1.3	4	14.0	12.0	4.0	2.3	0.9	1.5	98%
H. parvifolia (H-4)	135	3.0	2	29.5	8.8	2.5	2.4	1.1	1.3	96%
Hybrid (8x4)	132	2.5	2	33.0	11.0	4.7	2.3	1.1	2.1	23%
H. hel. ssp. *occidentalis* (H-3)	102	1.2	4	32.4	12.5	6.8	3.6	1.0	2.8	96%
H. hel. ssp. *helianthoides* (H-5)	135	2.5	0	6.5	11.5	5.6	2.8	0.9	1.5	99%
Hybrid (3x5)	108	1.7	3	26.2	13.4	6.3	3.2	1.0	2.2	95%
H. hel. ssp. *helianthoides* (H-5)	135	2.5	0	6.5	11.5	5.6	2.8	0.9	1.5	99%
H. hel. ssp. *scabra* (H-8)	125	1.3	4	14.0	12.0	4.0	2.3	0.9	1.5	98%
Hybrid (5x8)	125	1.3	3	12.2	11.5	5.1	3.2	0.9	1.8	93%
H. hel. ssp. *helianthoides* (H-5)	135	2.5	0	6.5	11.5	5.6	2.8	0.9	1.5	99%
H. parvifolia (H-4)	135	3.0	2	29.5	8.8	2.5	2.4	1.1	1.3	96%
Hybrid (5x4)	133	3.1	2	19.0	11.0	4.3	2.5	1.0	1.8	30%
H. parvifolia (H-4)	135	3.0	2	29.5	8.8	2.5	2.4	1.1	1.3	96%
H. rubra (H-16)	98	3.4	3	48.6	9.2	4.2	1.8	1.0	1.6	98%
Hybrid (4x16)	120	2.8	2	43.2	12.5	6.8	3.6	1.0	2.8	96%
H. hel. ssp. *occidentalis* (H-3)	102	1.2	4	32.4	12.5	6.8	3.6	1.0	2.8	96%
H. hel. ssp. *scabra* (H-8)	125	1.3	4	14.0	12.0	4.0	2.3	0.9	1.5	98%
Hybrid (3x8)	122	1.7	4	19.5	12.3	4.7	2.8	0.9	2.0	88%

*All characters expressed as mean values from five plants.

rather than of a single dominant one. In crosses involving other taxa, these same characters which appear dominant in the above cross are intermediate. *H. helianthoides* ssp. *occidentalis* × *H. rubra* and the cross, *H. helianthoides* ssp. *occidentalis* × *H. annua*, produced a few seeds by repeated crossings but germination failed.

H. helianthoides *ssp.* scabra *X* H. parvifolia.—This hybrid exhibited lower pollen viability than the hybrid between *H. helianthoides* ssp. *occidentalis* × *H. parvifolia*, averaging about 20 to 25 percent. When *H. parvifolia* was used as the egg parent, pollen viability averaged 25 percent, slightly higher than the reciprocal cross, which was 20 percent. This difference appears insignificant but was repeatedly observed. More striking reciprocal differences in sterility of hybrid pollen have been reported by Grant (1950) in *Gilia*.

Meiosis was observed in approximately 50 pollen mother cells and was found to be regular.

H. helianthoides *ssp.* helianthoides *X* H. parvifolia.—The five hybrids grown from this cross exhibited 30 percent pollen viability, slightly higher than ssp. *scabra* × *H. parvifolia.* No irregularities were observed in any stage of meiosis. In practically all characters this hybrid is intermediate between the two parents (table 2). This hybrid morphologically resembles ssp. *scabra* very closely.

H. parvifolia *X* H. rubra.—Seven crosses, including reciprocals, were made between these taxa. Seed set was obtained only when *H. parvifolia* was used as the egg parent, and then only 10 fruits were obtained. The following spring four seedlings grew to maturity. Meiosis in the pollen mother cells of the F_1 hybrids was highly irregular, yielding bridges, fragments, and univalents. Quite frequently three bridges and four univalents were observed at the first meiotic anaphase. Pollen stainability was found to vary from 2 to 5 percent, and seed set was less than 1 percent. None of the seeds germinated the following season.

Leaf size and head width were greater in the hybrid than in either parent (table 2). This might be attributed to hybrid vigor. *H. rubra* has red pales while in *H. parvifolia* they are yellowish-brown. In all four hybrids the pales were yellowish-brown, suggesting that the red pale color in *H. rubra* is due to a recessive gene or genes. The hybrids resemble the egg parent, *H. parvifolia,* more closely than *H. rubra.*

All attempts to cross *H. annua* with other taxa under cultivation in the research garden failed.

Intraspecific Crosses in H. helianthoides

H. helianthoides *ssp.* occidentalis × *ssp.* scabra.—In this F_1 hybrid the leaf base-petiole angle and petiole length are greater than in either parent, while other characters are intermediate (table 2). Pollen viability was decreased to 88 percent, only a slight decrease from 96 percent in ssp. *occidentalis* and 98 percent in ssp. *scabra* (fig. 3). The cross was easily made, that is, the stigmas withered soon after pollen was applied and seed set was as high as in either parent. The chromosomes exhibited good pairing at meiosis. This hybrid resembles many specimens of northwest Missouri, southwest Iowa and northeast Kansas, a region in which the two subspecies overlap in their natural distributions. For this reason many herbarium specimens have been annotated as putative hybrids.

The two remaining crosses, ssp. *occidentalis* × ssp. *helianthoides* and ssp. *helianthoides* × ssp. *scabra,* were easily made in the research garden with a slight decrease in pollen viability of the hybrids. Most characters measured were intermediate between those of the two parents (table 2).

Discussion of Crosses

Although *H. parvifolia* and *H. rubra* exhibit several morphological similarities, they are geographically and reproductively isolated. Their artificial hybrids yield only 3 to 5 percent viable pollen which would be expected since meiosis is highly irregular. *H. parvifolia* appears more closely related to *H. helianthoides* since their artificial hybrids yield higher average pollen fertility (23 to 34 percent). *H. rubra* fails to cross with any subspecies of *H. helianthoides,* suggesting a closer relationship to *H. parvifolia* than to any other species used in this study.

There are apparently no reproductive barriers to crossing within the *H. helianthoides* complex. Hybrids have been easily made between the subspecies, and pollen fertility is almost as high as in the parental types.

H. helianthoides ssp. *scabra* resembles the hybrid between *H. helianthoides* ssp. *helianthoides* and *H. parvifolia* very closely, suggesting that ssp. *scabra* may owe its origin to hybridization of these taxa at some time in their evolutionary history.

H. annua repeatedly failed to cross with any other species grown in the research garden, indicating complete reproductive isolation.

Ornamental and Economic Importance

There are several named varieties of *Heliopsis* which are grown as ornamentals. The varieties available for this study were *Heliopsis Gold Everhart*, *Heliopsis Pitcheriana*, *Heliopsis scabra* var. *incomparabilis*, and *Heliopsis helianthoides* var. *zinnaeflorae*. All of these horticultural varieties, with the exception of *Heliopsis helianthoides* var. *zinnaeflorae*, were grown and observed in the research garden. Meiosis in pollen mother cells was examined and found to be regular.

The above named varieties are not included in the taxonomic treatment of the genus because their affinities could not easily be established. *Heliposis Gold Everhart* is very similar to *H. helianthoides* ssp. *occidentalis*, differing only in having about twice as many ray flowers. *Heliopsis Pitcheriana* is very similar to *H. helianthoides* ssp. *helianthoides*, differing in being slightly larger. *Heliopsis scabra* var. *incomparabilis* is obviously closely related to *H. helianthoides* ssp. *occidentalis*. From herbarium specimens of *H. helianthoides* var. *zinnaeflorae* it is apparent that it is also very close to *H. helianthoides* var. *occidentalis*.

The most striking differences between the horticultural varieties and the wild taxa are the larger size, greater number of ray flowers, and longer peduncles. These characters are those most likely to be selected by the horticulturist.

In 1943 and 1944, the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture isolated an insecticidal amide from the roots of a Mexican plant referred to as *Erigeron affinis* DC. In 1946, E. L. Little, Jr., of the Foreign Economic Administration, called attention to the confusion in the botanical classification of the Mexican "peritre del pais" ("native pyrethrum") and pointed out that the plant was actually *Heliopsis longipes* (Gray) Blake, common name "chilcaugue" or "chilcuan" (Martin, Acree and Haller, 1947).

Since 1944, a larger supply of roots has been obtained from Mexico which provided an abundance of the insecticidal amide (N-isobutyl-2, 6, 8-decatrienoamide). An investigation was undertaken by the United States Department of Agriculture to determine the insecticidal activity of *Heliopsis* native to the United States, and it was found that all of these taxa, namely, *H. helianthoides* ssp. *scabra*, *H. gracilis* and *H. helianthoides* ssp. *helianthoides*, particularly the roots, were toxic to house flies. The roots of *H. helianthoides* ssp. *scabra* were especially toxic to these insects (Gersdorff, 1950). The pungent isobutylamide, for which the Department of Agriculture has proposed the name "scabrin," is appreciably more toxic than pyrethrins to most insects.

Generic Relationships

The genus *Heliopsis* has been associated with *Zinnia*, *Philactis*, *Eclipta*, and *Sanvitalia* by virtue of their opposite leaves, pistillate, fertile, and persistent ray flowers, and hermaphroditic, fertile disk flowers. The major differences separating these species from *Heliopsis*, however, are striking; narrow and usually entire leaves, phyllaries in 3–5 series, 3-angled ray achenes, flattened disk achenes, and a pappus, if present, of 1-several teeth.

Taxonomy[4]

[4]The herbaria from which material has been available for study are indicated by the following abbreviations: PH—Academy of Natural Sciences of Philadelphia Herbarium; F—Chicago Natural History Museum (Field Museum); GH—Gray Herbarium, Harvard University; IND—Indiana University Herbarium including the C. C. Deam Herbarium; MO—Missouri Botanical Garden Herbarium; NY—New York Botanical Garden Herbarium; SMU—Southern Methodist University Herbarium; US—United States National Herbarium, Smithsonian Institution, Washington, D. C.; UC—University of California Herbarium, Berkeley; MICH—University of Michigan, Ann Arbor; MIN—University of Minnesota, Minneapolis; TEX—University of Texas Herbarium, Austin. The writer wishes to express appreciation to the curators of the above listed herbaria.

Heliopsis Persoon

Heliopsis Pers., Syn. 2: 473. 1807.
Callais Cass., Dict. Sc. Nat. 24: 327. 1822.
Helepta Rafin., Neogynt. 3: 1825.
Andrieuxia DC., Prodr. 5: 559. 1836.
Helenomoium Willd., *ex* DC. Prodr. 5: 551. 1836.

Roots perennial or annual, somewhat fleshy, fusiform; aerial stems erect and ascending, or prostrate, leafy, branched, glabrous or variously pubescent. *Leaves* opposite or rarely alternate, filiform, lanceolate, orbicular, ovate, ovate-lanceolate, deltoid or deltoid-ovate, glabrous or variously pubescent, margin irregularly dentate to nearly entire, nearly sessile or with petioles up to 3.5 cm. long. *Heads* usually rather large, 0.6–3.5 cm. wide, terminal and from axils of upper leaves, radiate and discoid. *Phyllaries* 2–3 seriate, herbaceous or coriceous, ovate-lanceolate to ovate, subequal, outer series often foliaceous and longer than disk. *Receptacle* rather broadly convex, often hollow; pales firm, conduplicate, persisting, light brownish-yellow, red or purple. *Disk-flowers* perfect, yellowish, brownish-yellow or purple; ray-flowers pistillate and fertile, yellow, orange-yellow, or purple, ovate-lanceolate to oblong-lanceolate, notched at the apex, persistent. *Achenes* of the disk-flowers fertile, quadrangular at apex, conical at base, glabrous or minutely pubescent, those of the ray-flowers triangular, outer surface convex, otherwise as the disk achenes. *Pappus* lacking or represented by 2–3 membranaceous teeth or merely a crenulate ridge.

Type Species: *Buphthalamum helianthoides* L. Sp. Pl. 2: 904. 1753.

Artificial Key to the Species

A. Pales of the disk red or purplish-black
  B. Rays yellow
    C. Peduncles 30–40 cm. long, heads 1.0–1.5 cm. wide, pales red, axils of lateral branches and leaves densely tomentose; Baja California, Mexico.....1. *H. rubra*
    C. Peduncles 5–10 cm. long, heads 0.6–0.8 cm. wide, pales purple, axils of lateral branches and leaves sparingly pubescent; Michoacan, Mexico....2. *H. brachactis*
  B. Rays purple, peduncles 2.5–5.5 cm. long, pales purplish-black, heads 0.3–0.5 cm. wide; Guerrero, Mexico.....3. *H. parviceps*
A. Pales of the disk yellow or yellowish-brown
  B. Plants prostrate or semi-prostrate
    C. Leaves ovate-oblong to generally orbicular, peduncles 12.0–15.0 cm. long, phyllaries 1.1–1.3 cm. long; southern Mexico.....4. *H. procumbens*
    C. Leaves lanceolate, peduncles 4.0–7.0 cm. long, phyllaries 0.7–0.8 cm. long; Peru .....5. *H. decumbens*
  B. Plants erect
    D. Rays 6–8
      E. Leaves glabrous, sessile or petiolate
        F. Leaves sessile, filiform. Coahuila, Mexico.....6. *H. filifolia*
        F. Leaves petioled, ovate to ovate-lanceolate.
          G. Plants 50–75 cm. tall, branched, petioles 2.5–3.5 cm. long; Mexico, Central and South America.....7. *H. buphthalmoides*
          G. Plants 30–40 cm. tall, usually monocephalous, petioles 0.8–1.0 cm. long; southeastern United States.....8. *H. gracilis*
      E. Leaves pubescent, petiolate
        H. Leaves orbicular or ovate-lanceolate, peduncles 9–20 cm. long.
          I. Leaves 1.0–2.3 cm. wide, 2.0–3.0 cm. long, heads less than 1.0 cm. wide, plants 30.0–35.0 cm. tall; San Luis Potosi, Mexico .....9. *H. longipes*
          I. Leaves 2.5–4.5 cm. wide, 4.5–9.5 cm. long, heads 0.8–1.2 cm. wide, plants 50.0–75.0 cm. tall; Mexico, Central and South America.....7. *H. buphthalmoides*
        H. Leaves deltoid to deltoid-ovate, peduncles 5.5–7.5 cm. long; Central Mexico.....10. *H. annua*
    D. Rays 10–18
      J. Achenes rugose to subtuberculate, tan or black
        K. Leaves deltoid-lanceolate, petioles 0.8–2.5 cm. long, achenes black, plants 30–40 cm. tall; southwest United States and northern Mexico .....11. *H. parvifolia*
        K. Leaves ovate to ovate-lanceolate, petioles 2.5–3.5 cm. long, achenes light tan, plants 50–70 cm. tall; north central Mexico to Bolivia..... .....7. *H. buphthalmoides*

J. Achenes smooth, brown to dark brown
L. Leaves lanceolate, 5.8–8.5 cm. long, 1.0–1.8 cm. wide, leaves and peduncles densely pilose; Colombia.....12. *H. lanceolata*
L. Leaves ovate-lanceolate to deltoid 8.0–12.0 cm. long, 3.0–6.0 cm. wide, leaves and peduncles glabrous to rough scabrous. Central and eastern United States.....13. *H. helianthoides*

1. **Heliopsis rubra** Fisher, Madrono 12: 152–155, 1954. (T.: *Carter & Kellogg* 3158 UC! Isotype IU!)

Erect or ascending annual, biennial or perennial herb in mountainous regions, annual in plains region, 50–75 cm. tall, branching nearly to woody base; *stems* 0.5–3.5 mm. thick, glabrous below, sparingly pubescent above, previous year's stems glaucous, periderm flaking with age; axils of lateral branches and leaves densely tomentose; internodes 3.5–6.5 cm. long; *leaves* 6.5–

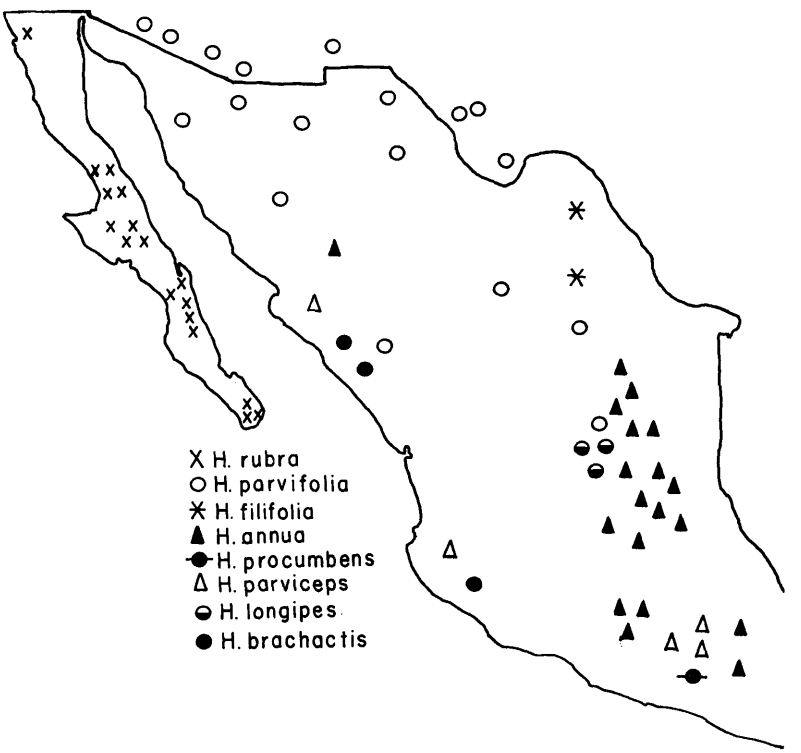

FIGURE 4. Distribution of Mexican species of *Heliopsis*.

12.0 cm. long, 3.5–5.0 cm. wide, firm, light green below, darker green above, petioles slender, 3.5–5.5 cm. long, tomentose, lower surfaces of blades glandular hirsute, densely strigose on the veins, upper surface glandular hirsute, rather scabrous, blades deltoid-rhomboid, apex acuminate, base attenuate to obtuse, margin nearly entire or sparingly dentate, teeth acute and mucronate; peduncles 30.0–40.0 cm. long; *heads* (excluding rays) 1.0–1.5 cm. wide (in fruit); *involucre* 2-seriate, phyllaries appressed, the outer unequal, oblong to oblong-lanceolate, apex acuminate to acute, densely velutinous to sericeous on the outer surface extending downward onto the upper limit of the peduncle; the inner phyllaries shorter and more acuminate; *rays* 8–10, 14–21 cm. long, 6–8 mm. wide, 13–15 nerved, yellow below at anthesis, reddish-orange above, becoming dull yellow with conspicuous greenish, sparingly pubescent nerves below and golden yellow above at maturity; disk corollas yellowish, lobes sparingly pubescent at the apex, tube 4.0–4.5

mm. long (at anthesis), obtuse; *pales* lanceolate-oblong to spatulate, glabrous, red at apex when young, becoming brownish-orange with age, membranaceous along the margins, 7.0–7.5 mm. long, 1.5–2.0 mm. wide; *ray achenes* triangular, outer surface curved, slightly puberulous when young, 4.0–4.5 mm. long, 2–3 nerved, surface irregularly tuberculate; *disk achenes* quadrangular, sharply so at the apex, rounded at the base, epappose or slightly ridged, faintly nerved on the angles.

Type locality.—Mexico: Baja California: Distrito del Sur, El Pulpito del Arroyo de las Parras, Sierra de la Giganta, lat. 25°58' N., long. 111°29' W., north-facing slopes, altitude 250 m.

Distribution.—Costal plains and mountainous regions of Baja California, Mexico (fig. 4). October to April.

In the past, herbarium material of *H. rubra* has been annotated as *H. parvifolia* which it resembles very closely and undoubtedly is its nearest relative. The chief separating characters are found in the leaf size, the shape to a lesser extent, and the color of the chaff.

According to Annetta Carter (correspondence), who has collected in the vicinity of the type locality on several occasions, *H. rubra* is a biennial or perennial herb in mountainous regions but grows as an annual in plains regions. In the mountains it usually occurs on north-facing slopes or breaks in vertical canyon walls. In years of good late summer rains it may be abundant in full sun on open plains, while in poor years these areas support little or no annual vegetation and may be covered with drifting sand.

2. Heliopsis brachactis Standl. *ex* Fisher sp. nov. (T.: *Leavenworth & Hoogstraal* 1370 MO!)

Herba annua, erecta; folia ovato-deltoidea, sparse pubescentia, 7.5–10.0 cm. longa, 3.0–4.5 cm. lata; petiolis 2.5–4.0 cm. longis, glabris; capitula 6.0–8.0 mm. lata, radii 4–5, aurei; corollae disci 2.0–3.0 mm. longae, purpurae, paleae 3.0–3.5 mm. longae, purpurae; achenia radii triangularia, 3.0–3.5 mm. longa, tuberculata; achenia disci quadrangularia 2.5–3.0 mm. longa.

Slender annual, 40–50 cm. tall; *stems* glabrous except in axils of upper leaves, 2.0–2.5 mm. thick, internodes 8.0–10.0 cm. long below, 3.0–5.5 cm. long above; *leaves* ovate to deltoid, firm, 7.5–10.0 cm. long, 3.0–4.5 cm. wide, crenate to subdentate, upper and lower surface slightly scabrous; *petioles* 2.5–4.0 cm. long, glabrous; *peduncles* of mature heads 5.0–10.0 cm. long, glabrous to minutely pubescent; *heads* small 6.0–8.0 mm. wide; *involucre* biseriate, outer phyllaries greenish, somewhat foliaceous, linear-oblong, inner oblong to obovate; *rays* 4–5, yellow, 5.0–6.0 mm. long, 2.0–3.0 mm. wide, commonly 2-cleft; *disk corollas* 2.0–3.0 mm. long, lobes purplish-black, *pales* 3.0–3.5 mm. long, suffused with purple at apex; *disk achenes* quadrangular 2.5–3.0 mm. long, dark brown, tuberculate, sharply angled, epappose; *ray achenes* obovoid, 3.0–3.5 mm. long.

Type locality.—Mexico: Michoacan: region of Tancitaro, 4 miles west of Apatzingan in semi-desert area, elevation 1200 feet. This species is known only from type locality.

Although *H. brachactis* differs strikingly from all other species in the genus, *H. parviceps* or *H. annua* seem to be the closest relative.

3. Heliopsis parviceps Blake, Proc. Biol. Soc. Wash. 33: 268, 1943. (T.: *L. H. MacDaniels* 128 F!)

Slender herbaceous annual, 45–60 cm. tall, with elongate branches above; *stem* light green, 1.5–1.8 mm. thick, striate; *leaves* small, ovate, 3.0–4.0 cm. long, 1.2–1.7 cm. wide, evenly hirsute on both surfaces, irregularly dentate to entire; *petioles* slender, 0.8–1.5 cm. long, pilose on the margins; mature branches with internodes up to 18 cm. long; *peduncles* 2.5–5.5 cm. long, glabrous to minute pubescent above; *heads* 0.3–0.5 cm. wide; *involucre* 2-seriate, phyllaries, 10–12, subequal 6.0–8.0 mm. long, the outer oblong, obtuse, 1.5–1.8 mm. wide, the inner broadly ovate, obtuse, all sparingly puberulous, strongly suffused with purple at maturity; *rays* 4–5, spreading, deep purple on both sides, finely papillate on both surfaces, margins inflexed forming a short tube or ring 3.0 mm. long above the achene, bluntly 3-cleft, 10–12 nerved, hispidulous on the nerves and the ring-like base; *disk corollas* deep purple, glabrous, about 3.0 mm. long, lobes ovate, acute, 0.6 mm. long; *pales membranaceous*, 3.5–4.5 mm. long, purple above, glabrous, keeled for ⅔ of the length from the base then broadly rounded and bluntly mucronate; ray achenes broadly obovoid, epappose, papillate and somewhat tuberculate, 3.0–3.5 mm. long, 2.3–2.5 mm.

wide, rounded on the outer face; *disk achenes* oblong, epappose, papillate to tuberculate, truncate at apex.

Type locality.—Mexico: Guerrero: along Cuernavaca-Taxco Road, 10 miles from Taxco, 5500 feet elevation.

Distribution.—Known only from the type locality (fig. 4).

This species is easily distinguished by its slender habit, small leaves, and purple disk and ray flowers. Although there are many differences, *H. brachactis* seems to be the nearest relative of this species.

4. Heliopsis procumbens Hemsl., Biol. Centr-amer. 2: 156, 1882. (T.: *M. Borgeau* 837 Kew, isotype GH!)

Prostrate creeping perennial herb, much branched, 20–25 cm. tall, leafy to base; *roots* thick, coarse, fibrous; *stems* 1.0–1.5 mm. thick, villous, internodes 2.0–2.5 cm. long; *leaves* orbicular or rarely ovate-oblong, 1.2–2.3 cm. wide, 2.0–3.0 cm. long, acute to obtuse at apex, lower and upper surfaces equally sericeous pubescent, sessile or with petioles to 5 mm. long, subterete; *peduncles* 12.0–15.0 cm. long, evenly sericeous pubescent; *heads* 0.9–1.2 cm. wide, 1.1–1.2 cm. high (as pressed); *involucre* 2-seriate, the outer phyllaries exceeding the inner, herbaceous, oblong, obtuse, glabrous, the inner more linear, acute tipped, glabrous; *rays* 8–10, 4.0–4.2 mm. wide, 0.8–1.1 cm. long, glabrous, golden yellow, irregularly 2–3 cleft; *disk corollas* 2.0–3.0 mm. long, glabrous, lobes golden yellow, obtuse; *pales* linear, 1.5–2.0 mm. wide, 3.5–4.0 mm. long, membranaceous along margins, keeled, acuminate; achenes epappose; *ray achenes* triangular, glabrous, smooth; *disk achenes* quadrangular, slightly tuberculate, tannish-brown when mature.

Type locality.—The handwriting on the label of the isotype is almost illegible, but appears to read "elevated pasture in forests, Desierta Vija." It is difficult to tell whether Disierta Vija is meant to indicate a city or a general locality. At any rate, the type locality was not located. Hemsley, in describing the species, presumably from the holotype, refers to Disierto Viejo of South Mexico. The holotype was not available for study by the writer, but Dr. H. J. Brodie, Botany Department, Indiana University, examined the type specimen and verified the description.

Distribution.—From north central Sinaloa south to Jalisco, southeast to the state of Mexico, at elevations up to 10,000 feet (fig. 4). June through September.

5. Heliopsis decumbens Blake, Proc. Biol. Soc. Wash. 53: 72, 1940. (T.: *W. H. Osgood* and *M. P. Anderson* 35 F!)

Low perennial herb with prostrate branching rhizome, short decumbent stems and long ascending or erect terminal peduncles; *stems* subterete, striate, pilose; internodes 5.0–10.0 mm. long; *leaves* ovate-lanceolate, 2.5–3.5 cm. long, 1.0–1.5 cm. wide, obtuse, cuneate, margin crenate-serrate, lower surface hirsute on main veins, sparingly so on smaller veins and other surfaces, densely hirsute on margins, upper surface glabrous or sparingly hirsute, *petioles* broad, 5.0–7.0 mm. long, pilose, obscurely margined to base; *peduncles* 4.0–7.0 cm. long, slender, pilose, with spreading or upcurved hairs, densely so beneath the head; *heads* 3.0–3.5 cm. wide, 1.5–2.0 cm. high (as pressed); *involucre* 2-seriate, outer phyllaries, 7.0–10.0 mm. long, oblong to oblong-ovate, obtuse, callose tipped, spreading to rather densely pilose with spreading or erect hairs, subindurate toward base, *inner phyllaries* 6.0–8.0 mm. long, obtuse or short acute, sparingly pubescent to nearly glabrous; *receptacle* (in flower) short, conical; *rays* 13–15, 1.0–1.3 cm. long, 0.3 cm. wide, golden yellow, oblong, 3-cleft, 11–14 nerved, hispidulous at the base; *disk corollas* yellow, glabrous, 4.0–6.0 mm. long; *pales* scarious, obtuse or acute, narrowly keeled, 3 nerved, about 6.0 mm. long; *ray achenes* obovoid-triangular, glabrous, epappose, 3 mm. long, 1.5 mm. wide, 1–3 nerved on each face, with narrow whitish irregular undulate margins; *disk achenes* obovoid, compressed, thickened, faintly three-nerved on each side, brownish to blackish, glabrous, epappose, quadrangular at the apex, 2.7 mm. long, 1.0–1.3 mm. wide.

Type locality.—Peru: Cajamaraca.

Distribution.—This species is known only from type locality. Although only a few specimens were available for examination, they are sufficiently distinct on the basis of its prostrate

habit, short peduncles and pubescence to warrant recognition as a species. It is impossible to ascertain its nearest relative from the few specimens available.

6. Heliopsis filifolia S. Wats., Proc. Amer. Acad. Sci. 25: 153, 1890. (T.: *C. G. Pringle* 2396 US!)

Erect perennial herb, 15.0–25.0 cm. tall, leafy branched to base; *stems* 1.5–2.5 cm. thick, glabrous, terete, smooth; internodes 1.5–3.0 cm long; *leaves* filiform, sessile, fascicled, opposite below, often alternate above, blade 2.0–2.5 cm. long, 1.0–1.5 mm. wide, pale green to straw-colored when dry, minutely strigose below, margin entire, apex obtuse; *peduncles* 13.0–30.0 cm. long, glabrous, terete; *heads* 1.5–2.0 cm. wide, 1.0–1.5 cm. high (as pressed); *involucre* 2-seriate, the inner phyllaries slightly exceeding the outer, tomentose along margins, 4–6 nerved, acute; *rays* elliptical, 1.5–1.8 cm. long, 1.0–1.5 cm. wide, 8–10 nerved, 1–3 cleft at apex, golden yellow, glabrous; *disk corollas* 6.0–6.5 mm. long, greenish-yellow below, bright yellow above, glabrous, lobes acute; *pales* 1.0–1.2 mm. wide, 1.0–1.2 cm. long, linear, 1–4 nerved, membranaceous along margins, brownish yellow above, apex broadly acute; *ray achenes* triangular, outer face curved, sparingly strigose, slightly rugulose, epappose; *disk achenes* quadrangular, truncate, rounded below, rugulose, strigose pubescent, epappose.

Type locality.—Mexico: Coahuila: Carneros Pass on limestone hills and ridges (fig. 4).

This relatively homogeneous species is very distinct by virtue of its filiform, sessile leaves, and glabrous peduncles. It is difficult to assign affinities to this taxon since there is only slight resemblance to any other species in the genus.

7. Heliopsis buphthalmoides (Jacq.) Dunal. Mem. Mus. Paris 5:56, 1819.

Anthemis buphthalmoides Jacq., Hort. Schoenb. 2: 13, 1797. (T.: British Museum.)

Heliopsis canescens Don. Bot. Reg. t. 7: 592, 1821. (T.: *Humboldt & Bonpland s.n.* Paris Museum).

Andrieuxia Mexicana DC. Prodr. 5: 559, 1836. (T.: Geneva Museum, Photograph examined US).

Perennial herb 50.0–75.0 cm. tall, much branched; *stems* terete, glabrous to pubescent above, pubescence often in two lines on opposite sides of the stem; intrenodes 7.5–12.5 cm. long; leaves ovate to ovate-lanceolate, cuneate to near truncate at base, 4.5–9.5 cm. long, 2.5–4.5 cm. wide, veins on lower surface sparingly to rather densely pubescent; *petioles* slender, 2.5–3.5 cm. long, sparingly to densely pubescent; peduncles 10.0–14.5 cm. long, essentially glabrous or pubescent in lines below the head; *heads* 0.8–1.2 cm. wide; involucre mostly 2-seriate, phyllaries oblong-lanceolate, acute to obtuse, essentially glabrous to villous, rarely leafy; *rays* 8–10, yellow, 2.5–3.0 cm. long. 0.5–1.0 cm. wide, linear-oblong, irregular 3-cleft; disk corollas yellowish-brown; *pales* linear-oblong, yellowish-brown; *achenes* tan to light brown at maturity, rugose, obovoid, epappose.

Distribution.—This species has, by far, the most widespread distribution of any in the genus, ranging from north central Mexico south through Central America into South America as far as central Bolivia (fig. 5). It has been collected at altitudes ranging from 600 to 10,000 feet.

Heliopsis buphthalmoides is a wide-ranging species and, as might be expected, there is considerable variation, particularly in leaf shape and amount of pubescence. Until more material from South America is available, it seems advisable to place *H. canescens* in synonomy with *H. buphthalmoides* since the diagnostic characters utilized in the original description fail to separate the two taxa clearly.

Heliopsis canescens was described from material collected and observed by Humboldt and Bonpland in the vicinity of Loxa, near Quito, Ecuador. Their reason for giving the taxon specific status was based on the nature of the pubescence of the leaves, upper stems and involucre. These characters are not consistent throughout the range of the species. Generally the pubescence of this taxon is most dense in the southernmost portion of the range and becomes less dense in the tropical portions of South America and Central America. Finally, in the northernmost portions of the range in Mexico, the taxon is nearly glabrous. It has also been observed that the truncate leaf shape is more generally found in specimens with the greatest amount of pubescence.

H. buphthalmoides resembles no other species in Mexico, Central or South America. It is morphologically more closely related to *H. helianthoides* of the United States in general habit, leaf shape, and size.

8. Heliopsis gracilis Nutt. Trans. Amer. Phil. Soc. N. S. 7: 353, 1841.
Heliopsis laevis var. *gracilis*. Torrey and Gray, Fl. No. Amer. 2: 303, 1842.

Erect perennial herb, 30–40 cm. tall, slender, unbranched to sparingly branched; *stems* 1.0–1.5 mm. thick, glabrous, smooth; *leaves* ovate-lanceolate to lanceolate, 4.5–5.5 cm. long, blade 1.8–2.0 cm. wide, light green below, deep green above, lower surface glabrous, upper surface sparingly strigose, more dense along margins, blade somewhat cuneate at base, acuminate at the

FIGURE 5. Distribution of *H. buphthalmoides*.

apex, nearly regular dentate, teeth averaging 1.0 mm. long, *petioles* 0.8–1.0 cm. long, glabrous to sparingly pubescent, somewhat subterete; *peduncles* 15.0–22.0 cm. long, glabrous below, minutely pubescent above; *heads* small, 1.0–1.2 cm. wide, 0.7–1.0 cm. high (as pressed); *involucre* 2-seriate, minutely pubescent on back, becoming more dense along margins, the outer phyllaries slightly foliaceous, spreading, linear-oblong, obtuse at apex, the inner phyllaries shorter, linear, obtuse; *rays* 6–8, linear, glabrous, 5.0–8.0 mm. wide, 1.8–2.2 cm. long, 1–3 cleft at apex, golden yellow; *disk corollas* 3.5–4.0 mm. long, throat pale brownish-yellow, glabrous, lobes dull yellow; pales lanceolate, keeled, 0.8–1.0 cm. long, obtuse; *achenes* glabrous to minutely pubescent on margins, dull brown, pappus a laciniate crown or 1–3 pointed teeth, ray achenes triangular; *disk achenes* quadrangular.

Type locality.—The type specimen is thought to be deposited in the British Museum and was not available for study. From a note penned on a herbarium sheet by Asa Gray, and by information obtained from the original description, the type locality must be in the southeast United States, probably Florida, Georgia, or Alabama.

Distribution.—From southwest Georgia west through north central Florida to southern Alabama (fig. 6).

The original description adequately agrees with the specimens examined except for a ref-

erence made concerning the indument of the leaves and peduncles which is described as being scabrous or smooth. The description may have been compiled from a single plant specimen. All the herbarium specimens examined are glabrous, or essentially so, certainly not scabrous. The most logical explanation of this discrepancy lies in the fact that the range of the species, as cited in the original description, is Georgia to Louisiana to Arkansas. This range would overlap that of the newly described taxon *H. helianthoides* ssp. *scabra*, which does have scabrous leaves. All specimens from Louisiana to Arkansas have been determined *H. helianthoides* ssp. *scabra*, not *H. gracilis*. Therefore the original description by Nuttall may have been broadened to include those plants which are now determined *H. helianthoides* ssp. *scabra*.

Heliopsis gracilis was not grown or observed in the living condition during this investigation. Morphologically, *H. gracilis* resembles *H. helianthoides* ssp. *helianthoides* in most respects except for size, ecological preference and non-branching habit. This species has been reported most often growing in well shaded areas, namely pine barrens.

9. Heliopsis longipes (Gray) Blake, Contr. U. S. Nat. Herb. 22: 608, 1924.
Philactis longipes Gray, Proc. Amer. Acad. Sci. 15: 35, 1879. (T.: *C. C. Perry & E. Palmer* 465 F!)

Subdecumbent or erect perennial herb, sparingly branched from the base; roots thick, coarse, fibrous; *stems* 1.0–1.5 cm. thick, glabrous below, sparingly to densely scabrous above; internodes 2.0–5.5 cm. long; *leaves* 2.0–3.0 cm. long, 1.0–2.3 cm. wide, oblong-lanceolate to elliptical, *petioles* 1.0–2.5 mm. long, strigose, blades irregularly dentate to entire above, about equally acute to obtuse at apex; *peduncles* 9.0–20.0 cm. long, sparingly pubescent below to densely pubescent above; *heads* (immature) 0.6–0.9 cm. wide, 0.9–1.2 cm. high; *involucre* 2-seriate, outer phyllaries densely pubescent on back, glabrous on inner side, obtuse, the inner phyllaries shorter, glabrous, acuminate at apex; rays 6–8, linear-oblong, 2–3 cleft, about 0.3 cm. wide, 1.0–1.2 cm. long, sparingly pubescent on back, yellow; *disk corolla* about 3 mm. long, glabrous, brownish-yellow above; *pales* linear-lanceolate, yellowish-brown, about 1.0 mm. wide, 1.0 cm. long, faintly 4 nerved, acuminate, glabrous; *ray achenes* (immature) triangular, glabrous; *disk achenes* (immature) quadrangular, glabrous, epappose or pappus of 2–3 minute, membranaceous awns.

Type locality.—Mexico: San Luis Petosi: Altitude 6000–8000 feet.

Distribution.—Known only from San Luis Potosi, Mexico (fig. 4).

Only three herbarium specimens were available for study but the taxon appears distinct by its small lanceolate-oblong, strigose leaves with very short petioles. It is further characterized by having rather long peduncles with small heads.

10. Heliopsis annua Hemsley, Biol. Centr. Amer. Bor. 2: 56, 1881. (T.: *Coulter* 358 Kew)

Erect, annual herb, much branched, 25.0–40.0 cm. tall; *stems* 2.5–4.5 mm. thick, striate, sparingly pubescent in vertical lines above; internodes 5.0–12.0 cm. long; *leaves* deltoid to ovate, 4.5–7.7 cm. long, 2.2–4.0 cm. wide, pale green below, light green above, sparingly pubescent below and above, margin irregularly dentate or crenulate to entire above; *petioles* long and slender, 2.5–3.5 cm. long, *peduncles* 2.5–7.5 cm. long, striate with two vertical lines of pubescence to apex, essentially glabrous elsewhere; *heads* 1.0–1.5 cm. wide, 0.8–1.2 cm. high; *involucre* 2-seriate, the outer phyllaries somewhat spreading and foliar, linear-oblong, acute and submucronate, pubescent on outer surface and margin, inner surface glabrous, the inner phyllaries membranaceous, 2–3 nerved, pubescent on margins, obtuse; *rays* 8–10, yellow, 5.0–6.0 mm. wide, 1.0–1.5 cm. long, 7–10 nerved on back, apex irregularly 3-cleft; *pales* 2.0 mm. wide, 5.0–7.0 mm. long, glabrous, faintly keeled, membranaceous, obtuse, cream yellow at apex; *ray achenes* triangular, epappose, outer surface convex, rounded at base, truncate at apex, glabrous, subtuberculate; *disk achenes* quadrangular, epappose, abruptly truncate at apex, glabrous below, sparingly pubescent above.

Type locality.—Mexico: Zacatecas: near Zacatecas.

Distribution.—Mexico: Southeast Sonora south to Michoacan and Queretaro, north to San Luis Potosi (fig. 4). July through September.

Dr. H. J. Brodie, Botany Department, Indiana University, examined the type specimen at Kew and found it to agree with the description. The taxon is distinct and easily recognized

by its many, compact showy heads on rather short peduncles, and the soft evenly pubescent leaves. In some localities this annual species is a weed in gardens and fields, whereas in other localities it is rather rare. Some collections indicate that it grows at altitudes of 7,000 meters. In the research garden at Indiana University, it exhibited prolific growth, spreading over an area of 3 to 4 feet. The attempted production of artificial hybrids with *H. parvifolia*, *H. rubra*, and *H. helianthoides* was unsuccessful. The taxon is relatively homogeneous. Its nearest relative seems to be *H. parvifolia* although it differs strikingly.

11. Heliopsis parvifolia Gray, Smithson. Contr. Knowl. (Pl. Wright.) 2: 86, 1853. (T.: *C. Wright* 1218 NY!)

Erect perennial herb, 30–40 cm. tall, slender; *stems* 1.5–4.0 mm. thick, glabrous or sparingly pubescent below, striate; internodes 1.5–7.5 cm. long; *leaves* deltoid-lanceolate, approaching deltoid-ovate, blade 1.5–5.5 cm. long, 0.8–1.5 cm. wide, light green below to deep green above becoming straw colored when dry, both surfaces sparingly pubescent to nearly glabrous, margin irregularly dentate to nearly entire, the lowermost teeth usually larger and irregular, decurrent or tapering abruptly onto petiole, apex acuminate to obtuse, *petioles* 0.8–2.5 cm. long, slender, puberulous; *peduncles* 8.5–20.0 cm. long, pubescent, apex more or less enlarged and hollow; *heads* 1.2–2.0 cm. wide (as pressed), disk 0.8–1.0 cm. high; involucre 2-seriate, the outer phyllaries exceeding the inner, oblong to oblong-lanceolate, apex acuminate, 4–6 nerved, densely pubescent on margins; *rays* 9–11, 1.2–1.4 cm. wide, 2.7–2.9 cm. long, oblong-ovate, 7–9 nerved, 3-cleft, glabrous, golden yellow when young, pale yellow with age, *disk corollas* yellowish-brown, glabrous, 4.0–4.5 mm. long, lobes brighter yellow than tube, obtuse; *pales* lanceolate to oblong, glabrous, keeled, acuminate at apex, 8.5–9.0 mm. long, yellow tipped; *ray achenes* epappose, 4.5–5.0 mm. long, brownish-black, triangular, glabrous, rugulose, faintly nerved on each face; *disk achenes* epappose, quadrangular, brownish-black when mature, 4.0–4.5 mm. long.

Type locality.—Mexico: Sonora: Hillsides between Barbocomori and Santa Cruz.

Distribution.—Southwest Texas to southeastern Arizona, southward to Durango and east to Tamaulipas, Mexico (fig. 4). June through October.

The species appears to be relatively homogenous and can easily be identified by leaf characters. The lower teeth of the serrate leaf are large and long, giving the leaf a deltoid shape (fig. 1). In addition to this, the peduncles are among the longest in the genus, reaching 20 cm. and amounting to half the total height of the plant. Under cultivation in the Indiana University experimental gardens, this species shows extreme vigor, attaining approximately twice the size exhibited by herbarium material.

12. Heliopsis lanceolata Blake, Proc. Biol. Soc. Wash. 53: 71, 1940. (T.: *E. P. Killip* and *E. C. Smith* 17339 US!)

Erect or ascending perennial herb, 20.0–25.0 cm. tall; *stems* subterete, discolorous with glabrous purple sides, pilose in the angles, essentially glabrous elsewhere, internodes 2.5–10.0 cm. long; *leaves* ovate-lanceolate, 8.0–8.5 cm. long, 1.0–1.8 cm. wide, sparingly sub-appressed hirsute on both sides, longer hairs on the margins and the chief veins beneath, bases of the hairs sometimes glandular, blades irregularly dentate, teeth small, about equally green below and above, firm; *petioles* slender, 1.0–2.0 cm. long, densely pubescent on upper surface; *peduncles* solitary, slender, 14.0–27.0 cm. long, densely pilose with spreading or erect grayish-white hairs, increasing in density above; *heads* 2.8–3.0 cm. wide, 1.0–1.5 cm. high; involucre 2-seriate, the outer phyllaries unequal, oblong or oblong-lanceolate, acute, pilose, the inner phyllaries shorter, oblong, acute or acuminate, glabrous or slightly puberulous; *rays* 14–18, 6.0–8.0 mm. wide, 1.9–2.3 cm. long, bright yellow, oblong, bluntly 2–3 cleft, puberulous at the base, glabrous on back side; *disk corollas* yellowish-orange, 4.0–5.0 mm. long, glabrous; pales oblong-lanceolate, obtuse, glabrous, narrowly keeled, thickened toward the apex, brownish-yellow above, 3.5–4.0 mm. long; *achenes* epappose, *ray achenes* obovoid, triangular, faintly nerved, sparingly pubescent on the angles, 3.0–3.2 mm. long; *disk achenes* oblong, abruptly quadrangular, faintly nerved on the faces, dull glabrous, crenulate near the apex, 2.5–3.0 mm. long.

Type locality.—Colombia: Dept. of Santander: Eastern Cordillera, vicinity of Vetas, alt. 3100–3250 meters.

Distribution.—Known only from type locality.

The lanceolate leaves, discolorous, purple, and glabrous stems, large heads on densely pubescent peduncles are the outstanding characters of this species. Herbarium material is limited and has only been collected from the type locality.

13. Heliopsis helianthoides (L.) Sweet, Hort. Brit. 487, 1826.

Erect perennial herb, 1.0–1.5 mm. tall, branched or unbranched, *stems* terete, smooth (ridged when dry), glabrous or pubescent, 3.5–5.0 mm. thick; *leaves* lanceolate, ovate-lanceolate or deltoid-ovate, 7.0–12.0 cm. long, 3.0–6.0 cm. wide, glabrous to scabrous, *petioles* 0.2–3.5 cm. long, margin coarse, irregularly dentate; *peduncles* 9.0–25.0 cm. long, glabrous to scabrous; *heads* 0.9–2.5 cm. wide; *involucre* 2–3 seriate, phyllaries lanceolate to ovate, acute to obtuse, outer phyllaries usually foliar, yellow to orange-yellow above, 1.2–3.5 cm. long, 0.5–1.3 cm. wide, linear to ovate; *pales* 8.0–8.5 mm. long, 0.9–2.0 mm. wide, obtuse, membranaceous to slightly puberulous,

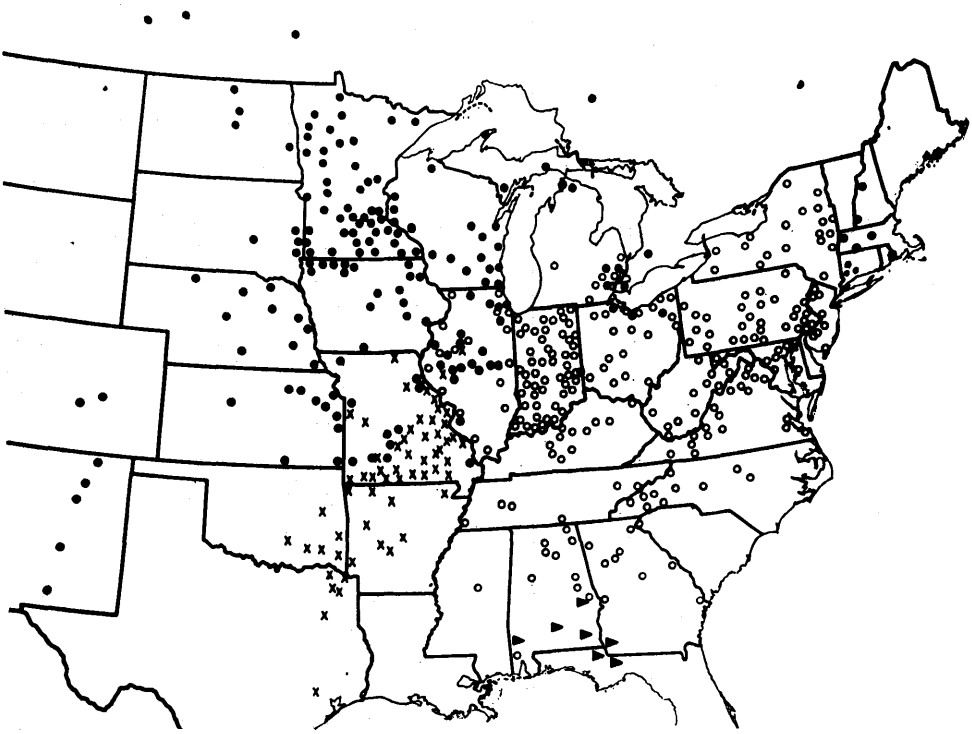

FIGURE 6. Distribution of *H. helianthoides* ssp. *helianthoides* (open circles); *H. helianthoides* ssp. *occidentalis* (solid circles); *H. helianthoides* ssp. *scraba* (x); *H. gracilis* (solid flags).

brownish-yellow at apex; *disk corollas* brownish-yellow; *ray achenes* triangular, outer surface convex, 3.0–3.5 mm. long, epappose or pappus represented by 2–3 membranaceous teeth, *disk achenes* quadrangular at apex, rounded at base, 3.0–3.5 mm. long, otherwise as ray achenes.

From an examination of the literature and herbarium material, it is evident that there has been a great deal of confusion in regard to the taxonomic status of this species. It is interesting to note the remarks made by Torrey and Gray in "Flora of North America" (1843): "We have so many forms intermediate between *H. laevis*, *H. scabra* and the very slender variety *gracilis*, that we unite them without the slightest hesitation; although the extremes appear abundantly different."

Heliopsis helianthoides consists of three distinct taxa with well defined centers of distribution,

namely the Appalachian region, the Ozark region and upper Great Plains region (fig. 6). Intergradation of characters occurs over a broad zone of hundreds of miles where the ranges of the taxa overlap (Fisher, submitted for publication). The hybridization study has shown that there are no reproductive barriers between these three taxa, and since they are morphologically distinct within their own centers of distribution, it seems advisable to reduce *H. scabra* Dun. and *H. helianthoides* (L.) Sweet to subspecies. Since the taxon of the upper Great Plains region has never been described, a new subspecies, *H. helianthoides* ssp. *occidentalis* has been proposed.

Because of the intergradation of characters, especially between ssp. *helianthoides* and ssp. *occidentalis*, annotation of herbarium material is extremely difficult. Those plants which closely resemble ssp. *occidentalis*, but have some characteristics of ssp. *helianthoides*, have been annotated as *H. helianthoides* ssp. *occidentalis* cline ssp. *helianthoides*.

Key to Supspecies of Heliopsis helianthoides

A. Leaves, peduncles and phyllaries glabrous to minutely pubescent, leaves ovate-lanceolate, 4.5–6.0 cm. wide, 8.0–12.0 cm. long, cuneate, heads 1.2–1.8 cm. wide, peduncles 5.5–8.0 cm. long ..... ssp. *helianthoides*

A. Leaves, peduncles and phyllaries scabrous, leaves deltoid or narrowly ovate-lanceolate.
  B. Leaves linear to ovate-lanceolate, 8.0–12.0 cm. long, 3.0–3.5 cm. wide, petioles 2.0–2.5 cm. long, head 1.2–1.4 cm. wide ..... ssp. *scabra*
  B. Leaves deltoid, 7.0–10.0 cm. long, 2.5–4.0 cm. wide, petioles 1.5 cm. long to nearly sessile, head 1.5–2.5 cm. wide ..... ssp. *occidentalis*

13a. Heliopsis helianthoides (L.) Sweet ssp. *helianthoides* Fisher comb. nov.

Buphthalamum helianthoides L. Sp. Pl. 904, 1753. (T.: Linnean Herbarium).

Silphium helianthoides L. Sp. Pl. 920, 1753.

Silphium solidaginoides L. Sp. Pl. 907, 1753.

Heliopsis laevis Pers. Syn. 2: 473, 1807.

Helepta grandiflora Raf. Neogynt. 3, 1825.

Helepta augustifolia Raf. Neogynt. 3, 1825.

Helepta parvifolia Raf. Neogynt. 3, 1825.

Heliopsis scabra var. *minor* Farwell, Mich. Acad. Sci. 19: 250, 1917. (T.: *Farweli* 4330 MICH!)

Heliopsis scabra var. *intermedia* Farwell, Mich. Acad. Sci. Rep. 19: 249, 1918. (T.: *Farwell* 4349 MICH!)

Heliopsis helianthoides var. *scabra* (Dun) Fernald, Rhodora 44: 340, 1942.

Heliopsis helianthoides var. *solidaginoides* (L.) Fernald, Rhodora 39: 456, 1937.

Stems glabrous; *leaves* ovate-lanceolate to ovate-oblong, 8.0–12.0 cm. long, 4.0–6.0 cm. wide, lower surface glabrous to sparingly pubescent, *petioles* 2.5–3.5 cm. long, glabrous; *peduncles* 9.0–13.0 cm. long, glabrous or slightly pubescent above; heads 0.9–1.5 cm. wide; *phyllaries* glabrous to sparingly pubescent; *rays* 10–12 pale yellow below, golden yellow above, 3.0–3.5 cm. long, 0.6–1.0 cm. wide.

Type locality.—"In America spetentrionalis, habitat in Virginia, Pennsylvania and Carolina." Linnaeus, Sp. Pl. 904, 1753. (Linnean Herbarium).

Distribution.—Eastern United States west to Indiana, Illinois, Kentucky, southeast to south central Georgia (fig. 6).

E. E. Sherff of Field Museum, Chicago, has distributed photographs of the type to several major herbaria of this country. On some of the photographs he has noted that the writing is in Linnaeus' hand. There is no question that the type description was drawn from the glabrous, smooth-leaved taxon of the Appalachian region.

This subspecies is centered in the Appalachian mountain region where it is relatively homogeneous. In the western portion of its range, however, namely Michigan, Indiana, and Illinois, there is a great deal of character intergradation with ssp. *occidentalis*. As a result, a broad zone of intermediate plants occur where the subspecies ranges overlap.

13b. Heliopsis helianthoides (L.) Sweet ssp. *occidentalis* Fisher ssp. nov. (T.: *O. A. Stevens s.n.* F! 885323, isotype UC 588923!).

Herba 1.0–1.5 m. alta; folia ovato-deltoidea, scabra, 2.0–4.0 cm. lata, 7.0–10.0 cm.

longa, petioli 0.2–1.5 cm. longi; pedunculati 12.0–25.0 cm. longi, sparse scabri; capitula 1.5–2.5 cm. lata.

Stems sparingly scabrous below to hispidulous scabrous above; *leaves* deltoid to deltoid-ovate, sparingly scabrous below, hispidulous scabrous above; *petioles* 0.2–1.5 cm. long, sparingly pubescent; *peduncles* 12.0–25.0 cm. long, sparingly pubescent below, densely scabrous above; *heads* 1.5–2.5 cm. wide, phyllaries scabrous; *rays* 12–15, pale yellow below, golden yellow above; 2.5–3.0 cm. long, 1.0–1.3 cm. wide.

Type locality.—North Dakota: Cass Co.: near Fargo in edge of thicket.

Distribution.—Southeastern Canada and northeastern United States west to Illinois, Wisconsin, Minnesota, the Dakotas and southern Saskatchewan south to Colorado and central New Mexico (fig. 6).

Much of the herbarium material of the Ozark region of Missouri, Arkansas, Oklahoma and Texas has been referred to as *H. gracilis* or *H. helianthoides*, while the taxon of the northern Great Plains has been referred to as *H. scabra*. *H. scabra* was described by Dunal from material collected along the Missouri River of the central and lower Great Plains Region of the United States. The exact type locality was not given but from the accompanying description it is obvious that he was not referring to the newly described taxon, *H. helianthoides* ssp. *occidentalis*, which is centered in the upper Great Plains region of Kansas, South and North Dakota, Nebraska and Minnesota. In addition to the scanty information in regard to the exact type locality, there is further evidence that the description was drawn from plants of Missouri or regions farther south because of reference made concerning the indument of the stems and the shape of the leaves. The original description states. "caulibus scabris, foliis scabris, ovate oblongo acuminate serratis . . ." Examination of several hundred herbarium specimens indicates that these characteristic features could not have been observed by Dunal from the taxon of the upper Great Plains region. This fact, unfortunately, was overlooked by taxonomists who have since published floras of the United States.

13c. Heliopsis helianthoides (L.) Sweet ssp. *scabra* (Dun.) Fisher comb. nov.
Heliopsis scabra Dun., Mem. Mus. Paris 5: 56, 1819.
Heliopsis laevis var. *minor* Hook., Comp. Bot. Mag. 1: 98, 1835.
Heliopsis laevis var. *scabra* (Dun.) Torrey and Gray, Fl. No. Amer. 2: 203, 1842.
Heliopsis minor (Hook.) Mohr, U. S. N. H. 6: 796, 1901.
Heliopsis helianthoides var. *scabra* (Dun.) Fernald, Gray's Manual of Botany, 8th ed: 1479, 1950.

Stems glabrous below, sparingly pubescent above; *leaves* lanceolate to ovate-lanceolate, sparingly pubescent below, scabrous above, *petioles* 2.0–2.5 cm. long, minutely pubescent; *peduncles* 11.0–17.0 cm. long, glabrous below, scabrous above; *heads* 1.2–1.4 cm. wide; phyllaries scabrous; *rays* 12–14, pale yellow below, orange-yellow above 1.2–1.4 cm. long, 0.5–0.6 cm. wide.

Type locality.—"Habitat Am. secus amnem Missouri." From the original description there is not doubt that the taxon referred to as *H. scabra* is typical of the plants of the lower Great Plains and Ozark region, the area from which the original plant must have been collected.

Distribution.—West central Illinois to southern Iowa, south to western Louisiana (fig. 6).

This subspecies is best separated from the others by the lanceolate or ovate-lanceolate leaves with long petioles. It can be further separated on the basis of pubescence, head size, and peduncle length.

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