

Synopsis of *Heliomeris* (Compositae)

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Introduction

Heliomeris was established by Nuttall (1848) based upon *H. multiflora*. Bentham and Hooker (1873) included *Heliomeris* in *Gymnolomia*, and the species now accepted as members of *Heliomeris* were treated under *Gymnolomia* by Robinson and Greenman (1899). Blake (1918), realizing that *Gymnolomia* was a highly unnatural genus, transferred several species to *Viguiera* as the section *Heliomeris*. Cockerell (1918), primarily on the basis of Blake's work, resurrected the genus *Heliomeris* and transferred all of the species of Blake's section *Heliomeris* to it. He also called attention to the color reaction of the rays of *H. multiflora* in caustic potash which is different from that of *Viguiera*, going on to say that, in spite of Blake's objections, he considered chemical characters as valid as morphological ones in taxonomic work. Until the present, Blake's treatment has been generally accepted. We feel, however, that there is justification for separating *Heliomeris* from *Viguiera*. Species of *Heliomeris* are characterized by having a weakly two-seriate, scarcely graduate involucre with herbaceous, generally lanceolate or linear-lanceolate phyllaries, whereas in *Viguiera* the involucre is two to seven-seriate, more conspicuously graduate, and the phyllaries are ribbed or indurate, at least at the base. Moreover, all species of *Heliomeris* are epappose; a few species of *Viguiera* may also lack a pappus but these are clearly related to other species that have a pappus. It may also be significant that all species of *Heliomeris* thus far counted have a base number of eight or nine chromosomes, whereas in *Viguiera* all species thus far known cytologically have a higher base number. *Heliomeris*, as here interpreted, comprises five species, limited to Mexico and the western United States.

A revision was finished some years ago (Yates 1967) and publication was delayed in the hope that additional field and herbarium study might be undertaken. Although this has proven possible only to a limited extent, it now seems desirable that some of the observations be put on record. For the most part only the name bringing synonyms and those synonyms not properly disposed of by Blake (1918) are included.

Chromosome Numbers

Several chromosome counts of $n = 8$ have been reported for three species of *Heliomeris*, and single counts of $n = 9$ and $n = 16$ have also been reported in *H. multiflora*. Counts for *Viguiera* are based on $x = 16$ or 17 (Federov, 1969; Moore, 1973, 1974) with the exception of *V. tenuis* which is $n = 12$ (Turner and King,

1964). It should be pointed out, however, that chromosome numbers have been reported for only 18 of more than 100 species of *Viguiera*.

H. multiflora. Since the first report of $n = 8$ (Heiser and Smith, 1955), this count has been verified many times. In the present study counts of $n = 8$ were obtained for *H. multiflora* var. *multiflora* from 16 different populations from Arizona, Colorado, New Mexico and Utah. Detailed citations may be found in Yates (1967); voucher herbarium specimens for these counts and the others reported here by us are deposited at Indiana University. Counts of $n = 8$ were also obtained for *H. multiflora* var. *nevadensis* in Coconino Co. (Yates 2094, 2099) and Yavapai Co., (Yates 2076), Ariz., and for *H. multiflora* var. *brevifolia* from Cochise Co., Ariz. (Heiser 63V7). Solbrig *et al.* (1972) report a count of $n = 8$ from California and $n = 16$ from Nevada for *H. multiflora* var. *nevadensis*, and Keil and Pinkava (1976) give counts of both $n = 8$ and 9 for *H. multiflora* from Arizona.

H. longifolia. A count of $n = 8$ was obtained for *H. longifolia* var. *longifolia* from Cochise Co., Ariz. (Heiser 6451), the same as has been reported by others (Heiser, 1963; Powell and Sikes, 1970; Solbrig *et al.*, 1972; Turner and Flyr, 1966; Turner, Powell and King, 1962). Counts of $n = 8$ were obtained for *H. longifolia* var. *annua* from Gila Co. (Yates 2107) and Yavapai Co. (Yates 2108), Arizona, and McKinley Co., New Mexico (Yates 2132). This agrees with the report from Navajo Co., Arizona by Keil and Pinkava (1976).

H. hispida. A count of $n = 8$ was obtained from material collected in Utah Co., Utah (Yates 71-U12). Keil and Pinkava (1976) have reported this species (as *Viguiera ciliata*) from Sonora as $n = 8$.

Hybridization

Artificial hybridizations were attempted with *H. longifolia* and *H. multiflora* in the greenhouse. The source of the material was as follows: *H. multiflora* var. *multiflora* (V4695), Bernalillo Co., N.M.; var. *nevadensis* (2094), Yavapai Co., Ariz.; var. *brevifolia* (63V7), Cochise Co., Ariz.; *H. longifolia* var. *longifolia* (6451), Cochise, Co., Ariz.; var. *annua* (2108), Yavapai Co., Ariz. Both species proved to be self-incompatible so emasculation was unnecessary. Considerable difficulty was experienced in securing germination of the seeds of the annual species and those hybrids with them as the maternal parent. The results are given in Table I.

Intervarietal hybrids of *H. multiflora* gave rather high pollen stainabilities, and, as would be expected, meiosis was normal. Hybrids of *H. multiflora* with the two varieties of *H. longifolia* showed highly reduced pollen stainabilities. Both sets of hybrids were largely morphologically intermediate between their parents and proved to be perennials. Meiosis was examined in both combinations. Eight bivalents were observed at diakinesis but abnormalities became evident at anaphase I. Most cells showed one, or occasionally more, chromatin bridges and one or more lagging chromosomes and possibly acentric fragments. It is likely that the abnormal disjunction is responsible for the sterility, although cryptic structural hybridity cannot be ruled out. The possible presence of acentric fragments along with the chromatin bridges suggests

heterozygosity for a pericentric inversion. Sister crosses of these interspecific hybrids gave no seed set, nor did backcrosses of the hybrids to the annual parents. However, in backcrosses of *multiflora* x *longifolia* to *multiflora* four seeds were produced in six heads. All seeds germinated; two of the seedlings died from damping off, but the other two survived to produce vigorous plants with pollen stainabilities of 77 and 80%. Eight filled achenes were secured in the backcross of *multiflora* x *annua* to *H. multiflora*, but the seeds failed to germinate.

TABLE I Results of hybridizations of *Heliomeris*

Combination	Number of hybrids	Pollen stainability	
		range	average
mult nev x mult mult	4	88-96	93
mult brev x mult mult	6	86-94	91
mult nev x mult brev	5	78-89	84
long ann x mult mult	6	7-33	18
long ann x mult brev	2	17,20	19
long ann x mult nev	7	4-14	8
long long x mult mult	8	12-34	25
long long x mult brev	7	7-33	23
long long x mult nev	2	37,43	40
long long x long annua	11	29-56	44

The artificial hybrids between the two varieties of *H. longifolia* also showed reduced pollen stainabilities (Table I), but the hybrids gave good seed set in backcrosses to both parents. Meiosis was similar to that described for the interspecific hybrids involving *H. multiflora* except that fewer cells showed bridges and lagging chromosomes.

Hybridization attempts were also made of the two species of *Heliomeris* with several species of *Helianthus* (*H. agrestis*, *H. debilis*, *H. niveus*, *H. Porteri*) and *Viguiera* (*V. adenophylla*, *V. cordifolia*, *V. dentata*, and *V. stenoloba*). No seeds resulted from any of the crosses.

Key to Species of *Heliomeris*

- a. Perennials with adventitious buds arising from woody caudex 1. *H. multiflora*
- a. Annuals usually lacking adventitious buds b.
- b. Leaves ciliate-margined on basal three fourths or throughout 3. *H. hispida*
- b. Leaves not ciliate-margined or only on basal one fourth c.
- c. Larger leaves crenate-dentate, oblong-ovate or oblong-lanceolate; known only from Veracruz, Mexico 5. *H. obscura*
- c. Larger leaves entire or serrulate, rhombic-ovate to linear-lanceolate d.

- d. Leaves linear-lanceolate to lanceolate; stems usually branched above and polycephalic; United States and Mexico 2. *H. longifolia*
- d. Lower leaves rhombic-ovate; stems branched at or near base giving rise to monocephalic branches; known only from Utah 4. *H. soliceps*
1. *Heliomeris multiflora* Nutt., Jour. Acad. Nat. Sci. Phil., ser. 2, 1:171. 1848. (LECTOTYPE: "Rocky Mountains," *Gambel*, GH!)

Typification of *H. multiflora* raises some questions. In the original description Nuttall cited two collections: Upper California, *Gambel* and Rocky Mountains, *Gordon*. A problem arises in that these two specimens may represent what are now considered two distinct varieties: plants from California and most parts of Nevada are characterized by having narrower leaves than those from the Rocky Mountains. Nuttall in his description states that the leaves are narrow and this could well apply to either variety. We have been unable to locate either a *Gambel* collection from California or a *Gordon* specimen in either BM or PH. Robinson and Greenman (1899) cite both collections in their revision. They state that they had examined specimens from GH and US, but neither specimen has been found at either of these herbaria. Blake (1918) indicated *Gambell* (sic) GH as the type collection. There are two sheets at GH, one of which is labeled "Gambel, Rio St. Juan, R. Mts," the other "Gambell, R. Mts." The latter sheet bears Blake's annotation label and can serve as the type in the absence of the specimens cited by Nuttall.

The perennation of *H. multiflora* is the most reliable character for distinguishing this species. When the basal part of the plant is lacking as with many herbarium specimens, it is often difficult to distinguish this species from *H. longifolia*. *H. longifolia* var. *longifolia*, however, often has longer leaves (more than 8 cm) and a thicker stem (more than 7 mm) than does *H. multiflora*. From *H. longifolia* var. *annua*, *H. multiflora* can usually be distinguished by its larger heads (more than 9 mm in diam.). It seems likely that hybridization must occur between the two species which may contribute to the difficulty of identification of some specimens.

Heliomeris multiflora is the most widespread and variable species in the genus. Four intergrading varieties may be recognized.

Key to Varieties of *H. multiflora*

- a. Larger heads (excluding rays) 1.4 cm or more in diam; leaves ovate-lanceolate; outer phyllaries exceeding head, reflexed 1a. var. *macrocephala*
- a. Larger heads usually less than 1.4 cm in diam.; leaves various; outer phyllaries seldom exceeding heads or only slightly so, erect to slightly reflexed b.
- b. Leaves ovate to elliptic, mostly alternate, apices obtuse, often with small mucro 1c. var. *brevifolia*
- b. Leaves lanceolate to linear, mostly opposite, apices acute, lacking mucro c.

- c. Leaves ovate-lanceolate to linear-lanceolate, margins not revolute 1a. var. *multiflora*
- c. Leaves linear to linear-lanceolate, margins revolute 1b. var. *nevadensis*
- 1a. *Heliomeris multiflora* var. *multiflora*.
Heliomeris multiflora var. *latifolia* Porter, U.S. Dept. Int., Misc. Publ. 4:72. 1874. (HOLOTYPE: Colorado, foothills near Colorado Springs, Porter, location unknown).
Heliomeris multiflora var. *genuina* Blake, Contrib. Gray Herb. 54:109. 1918.
 Southwestern Montana, eastern Idaho, western Wyoming, Colorado, Utah, eastern Nevada, western Arizona, New Mexico, Texas (Culberson Co.) and Mexico (states of Chihuahua, Durango, Jalisco, San Luis Potosí, Sonora, and Zacatecas). 1500-3350 m.
- 1b. *Heliomeris multiflora* var. *nevadensis* (A. Nels.) Yates, comb. nov.
Gymnolomia nevadensis A. Nels., Bot. Gaz. 37:271. 1904. (HOLOTYPE: Nevada, Meadow Valley Wash., L.N. Goodding 968, RM, dupls. at GH! US!)
Viguiera multiflora var. *nevadensis*, Blake, Contrib. Gray Herb. 54:110. 1918.
Heliomeris nevadensis Ckll., Torreya 18:183. 1918.
 New Mexico, Arizona, southwestern Utah, Nevada, and adjacent California, 1200-2400 m. This variety is sympatric with the previous one except in the western part of its range.
- 1c. *Heliomeris multiflora* var. *brevifolia* (Greene) Yates, comb. et stat. nov.
Gymnolomia brevifolia Greene ex Woot. & Standl., Contrib. U.S.N.H. 16:190. 1913. (HOLOTYPE: New Mexico, Socorro Co., Mogollon Mts., West Fork of the Gila River, Metcalfe 511, ND, dupls. at GH! US!).
Viguiera ovalis Blake, Contrib. Gray Herb. 54:110. 1918 (based on *G. brevifolia* Greene).
Heliomeris brevifolia (Greene) Ckll., Torreya 18:183. 1918.
 Utah (Beaver Co.), Arizona (Cochise Co.) and New Mexico (Socorro Co.), 2400-3050 m.
- The morphological study and the results of the artificial hybridizations indicate that this taxon is better treated as a variety than as a species. The plants are generally found growing in shaded areas. It was originally thought that the broad leaves might simply represent an ecological modification of phenotype, but plants of the accession grown in the full sun at Bloomington, Indiana, have maintained the distinctive leaf type.
- 1d. *Heliomeris multiflora* var. *macrocephala* Heiser, var. nov. Ab aliis varietatibus capitulis majoribus (1.4-2.0 cm diam) differt.
 Mexico: Chihuahua, "conifer forest on summit of Sierra Mohinora, 10,000-13,000 ft.," Correll and Gentry 23170 (HOLOTYPE, TEX). Same locality, Correll and Gentry 23145 (TEX). La Rocha, along tributary of Rio del Soldado, Sierra Mohinora, Correll and Gentry 23134 (TEX).

The most distinctive feature of this variety is its larger heads. Although the other phyllaries may somewhat exceed the disk and become reflexed in the other varieties, this tendency is most pronounced in var. *macrocephala*. The leaves are also broader than is usual in var. *multiflora* and var. *nevadensis*. *Correll and Gentry 23230* (TEX) from three miles south of La Rocha is somewhat transitional between var. *macrocephala* and var. *multiflora*.

2. *Heliomeris longifolia* (Rob. & Greenm.) Ckll., *Torreyana* 18:183. 1918.
Gymnolomia longifolia Rob. & Greenm., Proc., Bost. Soc. Nat. Hist. 29:92. 1899. (LECTOTYPE: "Western Texas," *Wright 328*, GH! [Blake, 1918])

Although Blake (1918) recognized *H. longifolia* and *H. annua* as distinct species and in spite of the reduced fertility in one cross between the two, it seems desirable to recognize these as varieties because of their extensive intergradation in Texas and parts of Mexico.

Key to Varieties of *H. longifolia*

- Some leaves usually 8 cm or more long; branching usually confined to upper half of plant; heads 9-14 mm in diam.; stem base usually more than 7 mm thick 2a. var. *longifolia*
 Leaves usually less than 8 cm long; plants much branched; heads 6-9 mm in diam.; stems slender 2b. var. *annua*

- 2a. *Heliomeris longifolia* var. *longifolia*
 Western Texas (Brewster, Jeff Davis and Presidio Counties), New Mexico (Hidalgo Co.), Arizona (Cochise Co.), and Mexico (states of Chiapas, Chihuahua, Durango, Michoacan, San Luis Potosi and Sonora), 600-2700 m
- 2b. *Heliomeris longifolia* var. *annua* (M. E. Jones) Yates, comb. nov.
Gymnolomia multiflora var. *annua* M. E. Jones, Proc. Calif. Acad. Sci. ser. 2, 5:698. 1895. (NEOTYPE: New Mexico, near Defiance, C. C. Marsh 229, US!)
Heliomeris annua (M. E. Jones) Ckll., *Torreyana* 18:183. 1918.
 Western Texas (Jeff Davis, El Paso and Presidio Counties), New Mexico (Dona Ana, Grant, Lincoln, McKinley, Sierra, Taos and Union Counties), Utah (Kane and Washington Counties), Arizona (Apache, Cochise, Coconino, Gila, Graham, Mohave, Pima, Santa Cruz and Yavapai Counties), Mexico (states of Coahuila, Chihuahua, Durango and Sonora). 600-2700 m

The original author did not designate a type for this variety. From his account, however, it is apparent that the description of the new variety came about as a result of his visit to the United States National Herbarium. Therefore, we have designated a neotype from among the specimens that he most likely examined.

3. *Heliomeris hispida* (A. Gray) Ckll., *Torreyana* 18:183. 1918.
Heliomeris multiflora var. *hispida* A. Gray, Pl. Wright. 2:87. 1853.

(HOLOTYPE: Mexico, Sonora, near Santa Cruz and San Bernardino, Wright 1222 GH!)

Gymnolomia hispida (A. Gray) Rob. & Greenm., Proc. Bost. Soc. Nat. Hist. 29:93. 1899.

Gymnolomia hispida var. *ciliata* Rob. & Greenm., Proc. Bost. Soc. Nat. Hist. 29:93. 1899. (LECTOTYPE: Beaver, Utah, Palmer 245 GH! [Blake, 1918])

Viguiera ciliata var. *ciliata* (Rob. & Greenm.) Blake, Contrib. Gray Herb. 54:114. 1918.

Viguiera ciliata var. *hispida* (A. Gray) Blake, Contrib. Gray Herb. 54:114. 1918.

Heliomeris hispida var. *ciliata* (Rob. & Greenm.) Ckll., Torreya 18:183. 1918.

Utah (Millard, Salt Lake, Sanpete and Utah Counties), New Mexico (McKinley and Santa Fe Counties), California (Los Angeles Co.) and Mexico (state of Sonora). 600-2100 m.

This species usually occurs in low damp pastures or meadows, sometimes bordering salt marshes, a habitat quite different from that of the other species. The distinctive pubescence readily sets this species apart from the others.

Two varieties have generally been recognized but there seems little justification to continue to do so, for they appear to differ only in degree of pubescence. The type collection comprises both the very densely pubescent form (var. *hispida*) and the less pubescent form (var. *ciliata*), as was noted by Gray in his original description. The former seems to be rare, for in addition to the type specimen the only other specimen approaching it is *Hasse s. n.* (US) from Santa Monica, California. This species is reported from Arizona (Kearney and Peebles, 1942) on the basis of *Thornber 97* (ARIZ, US) which we would refer to *H. longifolia*. The only recent collection of *H. hispida* that we have seen comes from Utah and possibly it is extinct in some of the other areas where it was known earlier.

4. *Heliomeris soliceps* (Barneby) Yates, comb. nov.

Viguiera soliceps Barneby, Leaf. West Bot. 10:316. 1966. (HOLOTYPE: Utah, Kane Co., Cottonwood Canyon, 1370 m., 41 miles southeast of Cannonville, Barneby 14435 NY!)

This species is known only from Utah. In addition to the type collection we have seen the following from near the type locality: *Reveal et al. 833*, NY; *Welsh and Welsh 12814*, *Welsh 11056*, *Atwood and Allen 02759*, *Atwood and Trotter 5073*, *Atwood 02759*, BRY. As pointed out in the original description the heads of this species are very similar to those of *H. longifolia* var. *annua* but it is very distinct in its vegetative characters from all other species. This species flowers in May and June, whereas all the other species of the United States usually flower much later.

5. *Heliomeris obscura* (Blake) Ckll. Torreya 18:183. 1981.

Gymnolomia obscura Blake, Proc. Amer. Acad. 51:515. 1916. (HOLOTYPE: Mexico, Veracruz, Maltrata, Kerber 211 BM, dupl. at US!)

Viguiera obscura (Blake) Blake, Contrib. Gray Herb. 54:115-116. 1918.

This very distinctive species is known only from the type collection. It does not appear to be particularly closely related to any other species of *Heliomeris*.

Excluded Species

1. *Heliomeris tenuifolia* A. Gray = *Viguiera stenoloba* Blake (fide Blake, 1918).
2. *Heliomeris simplex* Durand, Journ. Acad. Nat. Sci. Phil. Ser. 2, 3:91. 1855.

We have been unable to locate the type collection (California, *Pratten*) but the "disk corollas dark purple" given in the description excludes it from *Heliomeris*, all species of which have yellow disk corollas. Following the description, Durand states: "I have the same plant from the head of Rio Laguno, collected by Dr. Heerman...called by the Mexicans, 'Ojo de Gallo'." A specimen at PH, labeled "head of Rio Laguno [Laguna?], ojo d'gallio, Sept. 21, 1851" without collector being indicated, may possibly represent the specimen of which he wrote and it most likely comes from the Sitgreaves Expedition. Durand states that his species lacks a pappus, but this specimen definitely possesses a pappus. This specimen is probably an isotype of *Helianthus praetermissus*, E. E. Wats, which is known only from the type collection.

3. *Heliomeris Porteri* (A. Gray) Ckll., *Torreyia* 18:183. 1918 = *Helianthus Porteri* (A. Gray) Heiser, comb. nov.

This southeastern species was originally described as *Rudbeckia? Porteri* (HOLOTYPE: Stone Mountain, Georgia, *T. C. Porter*, GH!) by Gray (1849), who later placed it in *Gymnolomia* where it remained until Blake (1918) transferred it to *Viguiera*. In general aspect it is rather similar to the species of *Heliomeris*, but the only compelling reason for placing it in the latter genus is the epappose achenes. It is geographically isolated from all species of *Heliomeris*. This alone would not be reason for removing it from the genus. *H. Porteri* has a haploid chromosome number of 17, the same as found in many species of *Helianthus*, and unknown for *Heliomeris*.

Once *Heliomeris* is removed from *Viguiera* there is no justification for retaining this species in *Viguiera*. Moreover, there are no species of *Viguiera* in the southeastern United States. Crosses of *H. Porteri* have been attempted with a few species of *Viguiera* (Heiser, 1963; Yates, unpub.). A single hybrid was secured with *V. adenophylla*, but it was completely sterile and showed 34 univalents at diakinesis.

As this species does not seem at home in either *Heliomeris* or *Viguiera*, another genus must be found for it. The possibilities are to make it a monotypic genus or to transfer it to *Helianthus*. Either course of action might be justified, but we have decided on the latter, for it seems clear that its nearest relatives are to be found in *Helianthus*. Morphologically, it is presently excluded from *Helianthus* solely by the lack of a pappus, so once placed in this genus the generic description will have to be emended. Since the pappus of *Helianthus* is readily deciduous and serves no known function, its loss could hardly be considered a major evolutionary change. *Helianthus* is well represented in the southeastern United States, and it is there that another annual, *H. agrestis*, is found which is

certainly as distantly related to any other species of *Helianthus* as is *H. Porteri*. Moreover, artificial hybrids have been secured of *H. Porteri* with four species of *Helianthus*, and hybrids with *H. niveus* showed an average of 19% pollen stainability and up to ten pairs of chromosomes at metaphase I (Heiser, 1963). The evidence from the hybrids presently available would support its inclusion in *Helianthus*.

4. *Viguiera Shrevei* Steyermark, Field Museum Nat. Hist. **17**:421. 1938 (May 27) (HOLOTYPE: Mexico, Chihuahua, *Shreve 8035*, FM!) = *Verbesina longifolia* A. Gray, Proc. Amer. Acad. **19**:12. 1883 and so annotated by Steyermark on Oct. 29, 1938. In his description, however, Steyermark claimed that his new species apparently is closely related to *H. multiflora*.

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