

A REVISED CLASSIFICATION OF HELIANTHUS

C. B. Heiser, Jr.  
 Professor, Department of Botany,  
 Indiana University,  
 Bloomington, Indiana.

## Section I. Annuals and tap-rooted perennials. (Annual)

1. *H. similis*
2. *H. niveus* (including *H. tephrodes* and *H. canescens* as subspecies)
3. *H. debilis* (with 5 subspecies)
4. *H. praecox* (with 3 subspecies)
5. *H. petiolaris* (with 2 subspecies)
6. *H. neglectus*
7. *H. annuus* (see below)
8. *H. argophyllus*
9. *H. bolanderi*
10. *H. deserticola*
11. *H. anomalus*
12. *H. paradoxus*
13. *H. agrestis*
14. *H. ludens*

Species 2 through 12 form a "natural" group and hybrids between most of the species can be readily secured. The hybrids generally have highly reduced fertility and show a varying number of rings or chains at meiosis. All species are  $n=17$ . *Helianthus agrestis*, also  $n=17$ , of Florida, although a strict annual, has not produced hybrids with the other annuals in spite of numerous attempts. Living material of species number 1 and 14 has not been obtainable. Both are somewhat anomalous and are only tentatively included in this section. *Helianthus similis* is perhaps as close to *Viguiera* as it is to *Helianthus*. It is not definitely known whether the recently described *H. ludens* (Shinners, Sida 1: 377. 1964) is an annual or perennial. At present this species is known only from the type locality (Texas: Culberson Co. Lobo Flat, 19 miles east of Van Horn).

*Helianthus annuus* is the most widely distributed and the most variable species of this section. However, well defined geographical races do not exist. Several "varieties" may be distinguished.

Plants cultivated

- A. The monocephalic, large-seeded races cultivated for food or fodder.
- B. Branched forms cultivated for ornament, principally "doubled-flowered" and red-rayed forms.

Plants uncultivated

- C. Weeds of cities, etc., primarily central and eastern states.
- D. Rural weeds of the central states (Mo., Kan., Nebr., Iowa, etc.)

- E. Eastern Texas "race"
- F. Rocky Mountain "race"
- G. A small headed "race" of southern California, Nevada, and Utah.
- H. Unclassified forms of the western United States.

I have previously attempted to recognize some of these as botanical subspecies and other names are available in the literature, including some from Russia which have never been validly published. At present, I do not feel that the use of Latin names for this complex of intergrading races serves a useful purpose.

Helianthus argophyllus is clearly the species most closely related to H. annuus.

Section II. Perennials, primarily western North America. (Ciliares)

- 15. *H. gracilentus* (n=17)
- 16. *H. pumilus* (n=17)
- 17. *H. cusickii* (n=17)
- 18. *H. arizonensis* (n=17)
- 19. *H. laciniatus* (n=17)
- 20. *H. ciliaris* (n=34, 51)

Thus far it has been impossible to secure hybrids of members of this section with those of section III and the few secured with the annuals have been sterile. Hybrids have been secured between several of the species of section II. Morphologically, two groups are apparent in this section. The first three species share many features in common and are quite different from the last three which form a closely related group of species.

Section III. Perennials, primarily eastern and central North America. (Divaricati)

Series 1. "Divaricati."

- 21. *H. mollis* (n=17)
- 22. *H. occidentalis* (n=17)
- 23. *H. divaricatus* (n=17)
- 24. *H. hirsutus* (n=34)
- 25. *H. decapetalus* (n=17, 34)
- 26. *H. eggertii* (n=51)
- 27. *H. strumosus* (n=34, 51)
- 28. *H. tuberosus* (n=51)
- 29. *H. rigidus* (n=51)

Series 2. "Gigantei."

- 30. *H. giganteus* (n=17)
- 31. *H. grosseserratus* (n=17)
- 32. *H. nuttallii* (n=17)
- 33. *H. maximiliani* (n=17)
- 34. *H. salicifolius* (n=17)

- 35. *H. californicus* (n=51)
- 36. *H. resinosus* (n=51)
- 37. *H. schweinitzii* (n=51)

Series 3. "Microcephali"

- 38. *H. microcephalus* (n=17)
- 39. *H. glaucophyllus* (n=17)
- 40. *H. laevigatus* (n=34)
- 41. *H. smithii* (n=34)
- 42. *H. longifolius* (n=17)

Series 4. "Angustifolii" (all n=17)

- 43. *H. angustifolius*
- 44. *H. simulans*
- 45. *H. floridanus*

Series 5. "Atrorubentes" (all n=17)

- 46. *H. silphioides*
- 47. *H. atrorubens*
- 48. *H. heterophyllus*
- 49. *H. radula*
- 50. *H. carnosus*

Hybrids

- H. x multiflorus* (*H. annuus* x *decapetalus*)
  - H. x laetiflorus* (*H. rigidus* x *tuberosus*)
- (Numerous other natural hybrids known; best recognized by formulae)

The series recognized here are to some extent artificial. The assignment of species 42 and 50 is somewhat of a problem, and several of the polyploids probably have their ancestors from species of different series. Watson in his monograph of the genus recognized almost twice as many species as we do and some may think that we are recognizing too many, for hybrids between many of these species are as fertile as the parents and extensive intergradation occurs in nature (particularly with species 30-32 and 43-45).

Hybrids at any given ploidy level in this section generally show fairly regular chromosome pairing and little or only moderate impairment of fertility. Only a few hybrids of a diploid of this section have been secured with annual species and the plants were completely sterile. Hybrids between annuals and tetraploids are secured with difficulty as is the hybrid between *H. annuus* and *H. tuberosus*. Occasional hybrids have been reported from Europe in recent years but I hesitate to try to evaluate these since there is no way to be certain that the species reported are correctly identified. (Voucher herbarium specimens of all of my hybrids and the parental species are deposited in the herbarium of Indiana University).

Two of the most unusual species in the genus, *H. radula* and *H. carnosus*, are placed in this section. Both of these are southeastern and may have originated in Florida at a time when it was isolated from the mainland.

The tetraploid species most likely originated from hybridization and chromosome doubling of various diploid species of this section and probably should be considered segmental allopolyploids. The possibility exists that one of them, H. decapetalus, is a strict autopolyploid. The hexaploid species, in turn, probably originated from hybridization of a tetraploid with a diploid member of this group. Although, following Kostoff's work, it has generally been considered that H. tuberosus had a genomic constitution of  $A_1A_2B$  and that the B genome was similar to that of H. annuus, I no longer feel that this can be supported for several reasons. (1) There is no annual species that occurs within the range of wild H. tuberosus, although, of course, it is possible that the distributions were different at some time in the past. (2) All of the hexaploids of this section hybridize readily and produce fertile or nearly fertile hybrids. (3) There is no morphological evidence of an annual species in the hexaploids. (4) Since it is now known that annual genomes may give pairing with perennial genomes in certain combinations, Kostoff's finding of 34 pairs in the hybrid H. annuus x tuberosus does not necessarily support the hypothesis that an annual genome is present in H. tuberosus. I would suggest that H. tuberosus arose from hybridization of the tetraploid H. hirsutus (which can be hybridized with it) and a diploid species of this section. Experimental verification of this hypothesis has been hampered by the failure to secure seed germination of hybrids involving parents of different ploidy level as well as by the difficulty of inducing polyploidy by colchicine treatment.

The origin of H. tuberosus is one of the problems that needs additional study. Thus far chromatographic approaches have not been encouraging, but it is possible that other biochemical studies may reveal critical evidence of the origin. Among other problems calling for study is the nature of the nuttallii-giganteus complex in Canada where detailed field observations are lacking.

Section IV. South American, more or less shrubby, perennials. (Fruticosi)

This group of 18 species, mostly Andean, does not appear to be closely related to the North American species and may have had an independent origin from the genus Viguiera. The two species which have been examined are both diploid. (n=17)

#### PARTIAL BIBLIOGRAPHY

- Heiser, C. B., W. C. Martin, and D. M. Smith. 1962. *Brittonia* 14: 137-147.  
\_\_\_\_\_ and D. M. Smith. 1964. *Rhodora* 66: 344-358.  
\_\_\_\_\_. 1965. *Ann. Missouri Bot. Gard.* 52: 364-370.

DISCUSSION

Sackston: Have you looked over the species that occur naturally in this area of Manitoba and how many of them do you recognize and what do you call them?

Heiser: I am tempted to call my revision "A revision of the sunflowers of the United States and Mexico". I am calling it "A revision of the North American sunflowers", but I must admit I have never done any field work in Canada and one of the most perplexing problems is exactly what taxonomic disposition should be made of your Helianthus sub-tuberosus. It is somewhat intermediate between giganteus and eastern species in the States and Helianthus <sup>nuttallii</sup> microcephalus of the Rocky Mountains. I think it is a race of "Microcephali" and I am now calling sub-tuberosus a form of "Microcephali". We also have a brown disk diploid here which is my rigidus and you have maximiliani which is of course a northern race, Texas forms are giant things as expected, and I believe those are the principal perennial species here in Canada. You get decapetalus in Montreal I know and you get annuus and petiolaris barely coming up north of the Rockies. There are not many sunflowers in Canada.

Sackston: The tuberosus you agree, that what we call tuberosus is correct?

Heiser: Yes, that is tuberosus.

Sackston: There is no argument on maximiliani?

Heiser: No.

Sackston: Do you find natural hybrids between maximiliani and what we call sub-tuberosus here because in looking for disease material pathogens on them I found often things that to me looked remarkably like hybrid swarms of these two species? This is strictly visual observation without any taxonomic qualifications to support the comment.

Heiser: I have not seen this hybrid but I would expect it to occur. The species are closely related. They can be crossed readily and if they occur together you would expect hybrids. This is one of the difficulties in working out a classification of Helianthus because so many of these species hybridize and you get some of these hybrids and you don't know what to call them. This is one of the reasons Watson recognized so many of his species. Many of the things he saw he said, "Well this is different from this and different from that". He called it a species, actually it was a hybrid.

Sackston: What you are calling rigidus is what we get in the sandy areas around here west to Brandon, Carberry etc. On the basis of comments by Boivin in Ottawa we call laetiflorus var. subrhomboides. That is your rigidus, is it?

Heiser: Yes.

Sackston: Thank you very much.

Heiser: I have used this name, I haven't given all the origins. When and where this taxonomic revision will appear I am not yet certain but it would be within the next three years.

Sackston: Do you know of a species called lactiflorus?

Heiser: No, this is a misspelling of laetiflorus.

Sackston: I have had considerable arguments with Mme. Pustovoit on this lactiflorus business insisting that it was a misspelling of laetiflorus but she says that she has a laetiflorus and she has a different species which they call lactiflorus.

Heiser: There is no such species recognized in Kew index or in Watson. This, I think, probably came up as a misspelling or is an unpublished binomial from Europe. Some of the names published in Russia are not recognized by the official taxonomists because they have never been given latin descriptions or type specimens.

Sackston: I would guess from what I have seen of the publications etc. that this was an original misspelling, but it is also distinct from what she has as lactiflorus. Because she has been sent or given many collections which were obviously misidentified, she has two entities one of which is laetiflorus and one which she calls lactiflorus which are specifically distinct but the name may not be correct.

Heiser: Actually Helianthus laetiflorus - Dr. Clevenger and I have published on this in an early paper which is not cited here. We consider this is almost certainly a hybrid between tuberosus and rigidus. It is intermediate, we make the hybrid, we produce plants that look like this and have the same chromosome number and, of course, from this you can get backcrossing to both parents so you can pick up - actually you can have a continuum from tuberosus to rigidus and if you just grow isolated samples they look different. If you study the species throughout the entire range you can see all this degree of intermediate conditions and it is on this basis that we recognize it as a hybrid. Actually all hexaploids will hybridize readily and some people might say we should call tuberosus, rigidus, laetiflorus and ~~tomentosa~~ <sup>acutiflorus</sup> all one species. I think that would be carrying it to an extreme point though.

Sackston: Thank you very much.

Hoes: In respect to laetiflorus or lactiflorus it is not really a complete name is it - there also should be an author's name which could be a basis for deciding validity of the two names?

Heiser: For what, Helianthus laetiflorus?

Hoes: For both binomials. There should also be an author's name.

Heiser: I did not give the author's names on my list. You can get them from Watson's monograph or many of them I have named. I do not feel that we should perpetuate this practice of using the name in common gatherings or in titles. This is necessary for precision in published works but I

not going around and list L after all these species that Linnaeus named.

Hoes: The intention of my remark was as to the eventual confusion regarding laetiflorus or lactiflorus and whether a misspelling of one or the other has occurred. Does each binomial have the same author's name behind it?

Heiser: I have not seen it with the author's name. I believe in Bulgaria they give the name Pers. - which is also the authority for laetiflorus and which would be additional evidence of misspelling. I am not certain of that however. Excuse me, I did not understand you at first.

Mme. Pustovoit via Sackston: She said that she received the lactiflorus from Bulgaria and it was very strikingly different from the laetiflorus sub variety which she saw growing in my plots at Macdonald College and which I brought from Manitoba. I have the four perennial species which we commonly recognize in Manitoba growing at Macdonald. Mme. Pustovoit saw them there and found that the laetiflorus was quite distinct from the species she got as lactiflorus from Bulgaria.

Heiser: It does not alter my remarks. It was just a variation in what I call laetiflorus and the subrhomboides which is the extreme form of rigidus. It is a very small, nearly prostrate plant and is quite different from the rigidus we get in Iowa which is an erect plant and so on. I think you have to understand that variation is a rule in species. Some people want everything in one species to look alike but if you look around the room with the different hair color, eye color, no hair etc. this is all one species. We have great variability.

Mme. Pustovoit: The lactiflorus she received from Bulgaria is a tetraploid not a hexaploid.

Heiser: It is not laetiflorus then. Do you have a photograph of it?

Mme. Pustovoit: Yes, she has one here.

Heiser: I can't always identify sunflowers from a photograph but would be glad to try.

Mme. Pustovoit: The collections that they got from Bulgaria were quite badly mixed. As an example of this they received two lots which were the same species. One was designated lactiflorus and the other divaricatus.

Heiser: I think that the divaricatus, if I remember from your photographs, I would call decapetalus which would explain the 34 chromosomes

Sackston: What would you have called it?

Heiser: I think it is decapetalus.

Sackston: The trouble here is they certainly may have a distinct grouping but the names have been mixed in the sources of their seed supply.

Heiser: It is a very difficult genus taxonomically and, secondly, people from the U.S.D.A. do not always send plants out under their correct name.

Mme. Pustovoit through Sackston: Dr. Heiser, Mme. Pustovoit says she would like very much to be able to send you seed. She has good supplies of seed of all her 39 wild species and would like very much to send them to you to have your opinion of their specific positions.

Heiser: I would like that very much and I would be glad to send some to her in exchange but I no longer have living material of all these species that I am working with, only a limited number. If she would like more immediate identification if she sends me herbarium specimens it would mean that I would save a year. I would not have to grow them.

Mme. Pustovoit: She will send herbarium specimens.

\* \* \* \* \*