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THE SUNFLOWERS (GENUS HELIANTHUS) IN TENNESSEE[1]

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INTRODUCTION

The objectives of this study have been to determine (1) which species of the genus *Helianthus* (Family Compositae) occur within the boundaries of the state of Tennessee; (2) where each species occurs, on the basis of physiographic areas of the state; (3) the apparent ecological status of the species, *i.e.*, their distributions in relation to vegetation pattern and to inferred environmental factors; and (4) field characters, and an artificial key, enabling field identification of the species of *Helianthus* populations occurring in the state. Efforts have been made to recognize the taxonomic problems, with which any close observer of the members of the genus in Tennessee is faced in the field or herbarium, but the solutions to these problems have been beyond the objectives of this study, which has been concerned primarily with geographical considerations of the species and field recognition of the taxa represented in the state's vascular flora.

The study was undertaken in 1953, initially as a treatment of the genus *Helianthus* for inclusion in the "Flora of Tennessee" in preparation, with the intent that it would be based upon herbarium specimens already in the herbarium of the University of Tennessee and other institutional herbaria of the state. When the problems of interpretation of herbarium material became evident and the need for additional distribution records became apparent, field collections and observations of the genus were undertaken, and during the early part of the month of September of the years 1957, 1959, and 1961, nearly all counties of the state were visited. Collections of the genus made during these years were more geographically extensive than intensive, although many of them are population samples in which certain variations and extremes in morphological characters are evident. These, and field observations of the species of *Helianthus* populations, were made throughout the state wherever members of the genus were encountered on the landscape. All specimens are currently on file in the herbarium of the University of Tennessee, Knoxville. In addition to the collections made during the several years in which this study was intermittently in progress, all Tennessee specimens of the genus on file at the New York Botanical Garden, Gray Herbarium, and U. S. National Herbarium were reviewed.

Taxonomic interpretations of the Tennessee collections have been, for the most part, those of Dr. Charles B. Heiser, Jr., Indiana University, and Dr. Dale M. Smith, University of Illinois, between whom all of the Tennessee species of *Helianthus* specimens (except those of *H. angustifolius,* reviewed by Dr. William C. Martin, Jr., University of New Mexico) have been critically reviewed and annotated through the years of the study. The taxonomic phases of the study have been dependent upon their judgments and counsel, and it is hoped that as partial compensation for the time and efforts they have so unstintingly given to the problems presented by the University of Tennessee specimens, the 700 or so collections may serve as a contribution to understandings of the populations in this segment of the Southeast for the monographic work on this genus in preparation. In addition, their critical reviews of the manuscript resulted in a number of contributions to its final contents.

In some cases determinations of the Tennessee material have been modified from those made by Dr. Heiser or Dr. Smith, usually because of certain field observations made by the author at the time of collecting, and certain specimens in the University of Tennessee collection (and other herbaria) have been excluded from consideration in this treatment because of the too great uncertainty of correct epithets. The author, of course, accepts full responsibility for all errors in fact or misinterpretation herein recorded.

THE TENNESSEE SPECIES OF *HELIANTHUS*

The genus *Helianthus,* as known in eastern United States, is well represented in the state of Tennessee. Its species are the most conspicuous of the late summer- and autumn-flowering "showy" composites in most parts of the state. In regions where other composite genera with conspicuous yellow rays characterize the landscape at this season, the sunflowers are often uncommon or absent, particularly in areas where species of *Bidens* and *Chrysopsis* are common.

Although the Tennessee species of *Helianthus* include nearly all of the species now recognized in the northeastern and central states[2], certain ones more or less common to the North, Northwest, or West, appear to be present in Tennessee as sparingly introduced species *(H. giganteus, H. grosseserratus, H. maximiliani);* two are known in Tennessee from cultivated grounds or only rarely as escapes from cultivation *(H. annuus* and *H. laetiflorus),* and one is presumed to be cultivated

[1] Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. 215. Field work was supported by the University of Tennessee (in part by National Science Foundation Grants G-1478 and G-4446) during periods when the author was a staff member of the Department of Botany.

[2] Three species recognized by Fernald (8) are no longer considered valid: **H. doronicoides** Lam. (14), **H. trachelifolius** Mill. (personal communication, C. B. Heiser, Jr.), and **H. Kellermanii** Britt. (20). **H. tomentosus** Michx., included among the Tennessee species of **Helianthus** by Gattinger (10) on the basis of a collection by A. Ruth ("Lake Otase, near Knoxville") is a determination sufficiently doubtful in the absence of the supporting specimens that the species is not included here.

sometimes *(H. salicifolius);* one *(H. occidentalis)* is encountered so infrequently in the state as to make uncertain its status as a native species; one species believed likely to be native in the state is currently not supported by any herbarium specimens *(H. laevigatus).* The remainder *(H. atrorubens, H. silphioides, H. mollis, H. divaricatus, H. hirsutus, H. microcephalus, H. glaucophyllus, H. strumosus, H. decapetalus, H. tuberosus, H. angustifolius,* and *H. eggertii)* are the state's native sunflowers which have been reported to date and for which there are supporting specimens in one or more institutional herbaria. Of these, *H. glaucophyllus,* recently separated from *H. microcephalus* by Smith (29), is known in Tennessee from but two collections; *H. eggertii* is known from but three counties and from putative hybrids (or their derivatives) in three other counties; *H. decapetalus* appears to be essentially restricted to the mountains of East Tennessee; and the taxonomic status of *H. strumosus* in the state is in question. There are, therefore, eight species which constitute the members of this genus which are significant components of the plant communities of the state as a whole.

When compared with that of other regions, the vegetation of Tennessee appears to be as floristically rich with regard to representatives of the genus *Helianthus* as that of any state in central and eastern United States, and perhaps in this respect is richer than most. The magnitude of diversity and extremes of edaphic (geologic) and climatic conditions is probably unsurpassed within the boundaries of any other state east of the Rocky Mountains, and it would be surprising, therefore, if this, like any other relatively large genus of vascular plants indigenous to the Deciduous Forest region, would not here be well represented both in number of species and number of individuals. The open forests of Oak-Hickory and Oak-Pine and their variations, which have been prominently represented on the uplands of certain regions of the state for probably millions of years, are communities in which the environmental factors appear to be optimum for several native sunflowers. In addition, the creation of multitudes of forest borders and open abandoned lands, for which the sunflowers are generally well adapted, has resulted in a many-fold increase in the area of habitats permitting the invasion and establishment of members of this genus. The sunflowers do not occur, however, in locally extensive stands, as is true in other states known by layman and botanist alike for their sunflower-dominated landscapes in summer and autumn, but rather as more or less scattered small populations of a few to perhaps a few dozen individuals. They may be absent altogether from the landscape of well-defined areas in any physiographic region of the state.

It can be inferred that climatic regimes are the primary controls of the distribution of species occurring in the mountains of East Tennessee, but the regional occurrences elsewhere in the state of both the genus and its species, are evidently correlatable in most cases with edaphic factors since the patterns of distribution follow closely the patterns of outcrop of major bedrock types in the various physiographic areas of the state. They are most abundantly represented with regard to numbers of species and individuals in the sterile acid

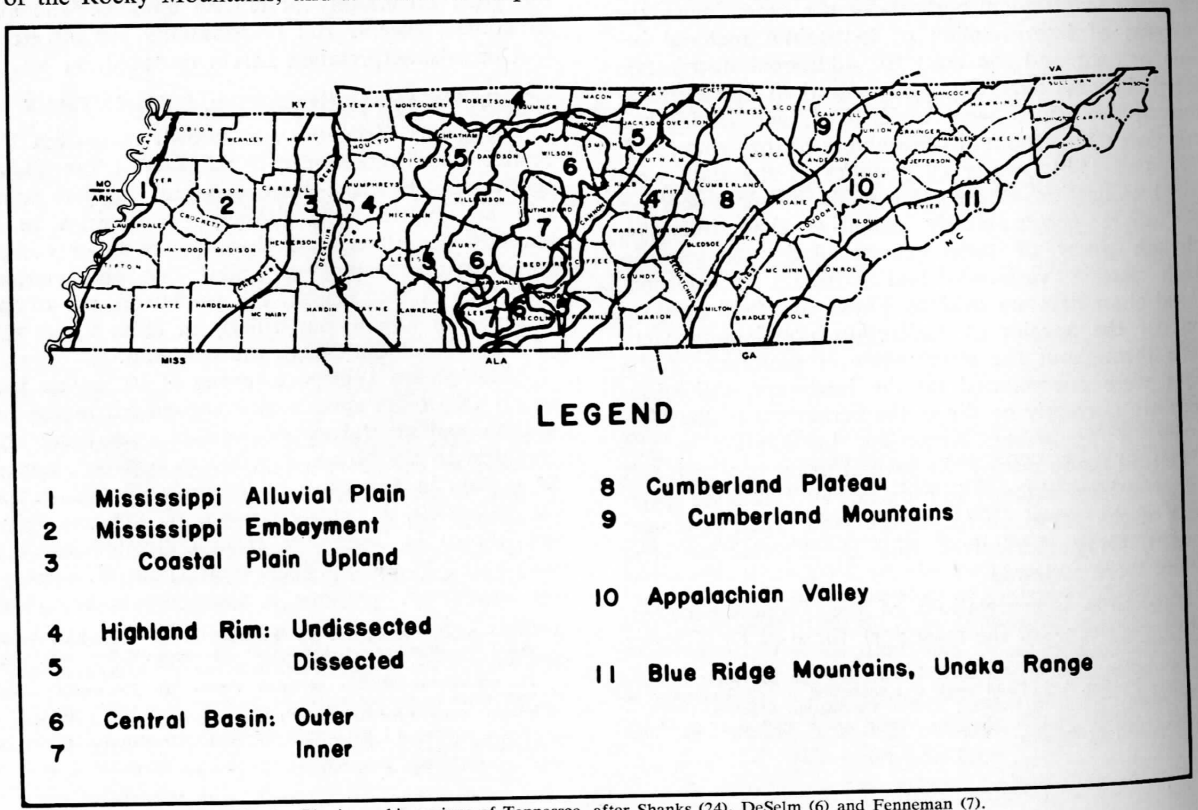


Fig. 1. Physiographic regions of Tennessee, after Shanks (24), DeSelm (6) and Fenneman (7).

soils of the Cumberland Plateau, Western Highland Rim and parts of the Eastern Highland Rim, and southern Mississippi Embayment (Fig. 1), especially in areas often referred to as "barrens" country, and least well represented in the calcic soils of the Central Basin and dissected Highland Rim.

In general, the species of *Helianthus* represented in Tennessee require high light intensity and well-drained soils, and as a group they have an apparent capacity for drought endurance. As with other herbaceous species of eastern United States, however, above-average rainfall during the growing season may result in exceptionally vigorous vegetative and reproductive growth. Within the genus there are exhibited varying degrees of shade tolerance and a wide range of inferable moisture-aeration requirements, so that representatives of the genus are associated with the most xeric habitats of the state, through the total range of soil-moisture levels to habitats in which soils are at least seasonally water-saturated. The species vary from those requiring full sunlight to those which grow in partial shade, and even to those which may grow under the closed canopies of mature forests. The genus remains, however, one occurring primarily on extremely to moderately xeric sites of the uplands, and where light intensity is not reduced, or reduced only moderately as along forest borders or in forests with open canopies.

The genus, as it occurs in Tennessee, has the following characters: Coarse herbaceous perennials (except for one annual), only the more or less elongate rhizomes or crown buds overwintering[3], sometimes tuber-bearing; stems from less than 1 m. to 4 m. high, solitary or colonial, simple except for the inflorescence branches, variously pubescent, scabrous, or glabrous, sometimes glaucous; leaves simple, opposite at least at the lowermost nodes and continuing to be opposite throughout or becoming alternate at the middle or upper nodes[4], rarely whorled below the inflorescence; blades varying in shape from linear-lanceolate to broadly ovate-suborbicular but mostly lanceolate or ovate, 3-veined but in some species obscurely so and in two species 1-veined, tips rounded to long-attenuate but most often acuminate, margins entire to sharply toothed but usually shallowly toothed, upper and lower surfaces smooth and glabrous to markedly rough-hispid or densely hairy, the amount and kind of pubescence most often intermediate between extremes, long-tapering into a petiole or petiole-like base, or (in most of the native species) more or less abruptly contracted into the petiole, and the blade then with a truncate or rounded base and the petiole more or less winged, or sometimes unmargined, sometimes sessile and cordate-clasping.

Inflorescence varying from one head (usually in depauperate individuals) to many branches bearing many heads (corymbose-racemose), the principal inflorescence branches originating from the axils of the uppermost leaves only, frequently from the middle nodes also, and occasionally the lower nodes as well; involucral bracts subequal, in 2-4 series, herbaceous, linear-lanceolate to broadly ovate, variously pubescent to essentially glabrous, often with ciliate or ciliolate margins, obtuse to long-attenuate at the tip, very loose and spreading to distinctly appressed, longer or shorter than height of the disk; rays more or less showy, pale to deep yellow, 5-30 (most commonly 8-15), 1-4 cm. long, flowers sterile though sometimes pistillate, in one series around the disk margin; disk 0.5-3 (—5 or more in *H. annuus*) cm. broad, receptacle flat or usually low-convex; disk flowers subtended by chaffy bracts enveloping the achenes, bisporangiate, fertile; the styles bifid, corollas tubular with yellow, purple or rarely reddish lobes; achenes glabrous, slightly compressed laterally with 2 prominent and 2 obscure angles, not winged or margined, the pappus of 2 readily deciduous awns on the principal angles and sometimes with accessory paleae.

Two species, *H. atrorubens* and *H. silphioides,* may be mistaken easily for members of the genus *Silphium,* in part because of their broad, obtuse, glabrous appressed involucral bracts which are like those of *Silphuim* and unlike those of any of the other species of *Helianthus.* In the genus *Silphium,* however, the ray flowers are pistillate with undivided styles, fertile, in 2-3 rows around the disk margin, and the achenes are dorsally compressed and distinctly winged; disk flowers are bisporangiate but sterile, and their corollas are never purple.

In any present-day study of the genus *Helianthus,* whatever its objectives or emphasis, the matter of hybridization necessarily becomes a subject of pre-eminent consideration. All who closely observe the sunflowers in the field (or as herbarium specimens) are impressed with their variability. The conspicious variations—some of them occurring only rarely, but nonetheless distinctive for their rarity—have been variously treated as new species or varieties, or as undeterminable. The suggestion that hybridization occurs among the perennial sunflowers was made in the limited but noteworthy treatments of the subject by Cockerell (4, 5) who concluded in 1919 that "It seems possible that in this genus the origin, through hybridization, of distinct plants, with the attributes of species, may be demonstrated." Watson (33), whose descriptive contributions in 1929 were the first invaluable efforts toward a monograph, carefully noted many distinctive variations throughout the genus; but that the explanations for these might lie in character recombinations following hybridization is scarcely suggested in his work.

That there are discernible patterns of variability and that these patterns are the consequences of certain inferable and experimentally demonstrable genetic relationships have been a major contribution to the understanding of the complex problems in the genus and to what may be effective approaches to their solution. Experimental hybridization and cytological studies reported by Heiser, Smith, Jackson, Guard, and Martin (see Literature Cited) have laid the foundations and

[3] Watson (33) reports that in **H. occidentalis** a flat rosette of leaves is produced in the autumn; if these overwinter, as do such leaves in many other Compositae, the character is of taxonomic value since it is not known elsewhere in the genus in central United States (1).

[4] According to Watson (33): "In all sunflowers, at least the first four or more leaves are opposite, and from here on they tend, more or less strongly according to the species, to become alternate. Vigor and luxuriance of growth are conducive to the alternate arrangement, and depauperation, even to a very slight degree, is favorable to the opposite arrangement. Drought, crowding, shade, poor soil, and mechanical injury are all favorable to opposite leaves."

elucidated many of the details upon which rest explanations of the specific and broad patterns of variability within the genus. Published studies by these investigators have dealt especially with species which on the whole are better represented in the vegetation of the Midwest than in that of the southeastern United States; but the principles relating to speciation, hybridization, introgression, and other evolutionary phenomena, which have been demonstrated by this group to have played roles of significance in the evolution of taxa in this genus, are probably no less applicable to the species of *Helianthus* and the evolutionary problems of the taxa which are more abundantly represented in Tennessee.

That hybridization and introgression between species have occurred at least as commonly in the state as has been found to be the case in the Midwest, there can be little doubt from the numerous problems of species determination which arise in the field. Most Tennessee sunflowers are diploid species (n=17), but tetraploid (n=34) and hexaploid (n=51) species are also represented (14). Among the polyploids *(H. hirsutus, H. decapetalus, H. strumosus, H. laevigatus, H. eggertii,* and *H. tuberosus)* are those species which present some of the most obvious variability and some of the most complex taxonomic problems in the Tennessee sunflower populations. It seems probable that Tennessee may offer exceptionally suitable research materials for future studies of the genus because of the state's evident great diversity of soils, climate, vegetation, and physiographic features, the excellent representation of the genus as a whole within its boundaries, its central geographic location with respect to the rest of central and eastern United States, and its ancient highlands, which have served as refugia and/or centers of endemism for vascular plants for many millions of years.

Experimental investigations have been beyond the scope of the present study. However, where suspected hybrids have been collected in the field, pollen stainability tests have been made, employing the anilin blue-lactophenol technique, with counts based on 200-500 pollen grains obtained from undehisced anthers. To what extent the percentage of stainable pollen can be used as a basis for inferences of hybridity or genetic "pureness" of individuals in Tennessee populations is in doubt. That F_1 hybrids of morphologically distinct species can produce pollen whose stainability approaches 100 percent has been demonstrated a number of times (17, 18, 19), and the high percentages of such pollen which may occur in members of apparent hybrid swarms in Tennessee may support the findings of all of these investigators that there is generally a rather high degree of chromosome homology among diploid members of the genus, especially within a given section of the genus. Moreover, that individual plants, unsuspected of being hybrids or hybrid derivatives from either their morphological characters or the character of the field populations from which they came, may bear pollen with very low percentages of stainability is apparent from certain of the counts made on Tennessee plants during the present study. In certain cases, however, the pollen viability is of interest, at least as corroborative evidence of the hybrid nature of populations or individuals whose morphogenetic characters already mark them as unquestionable hybrids.

Since hybridization and introgression result in individuals or populations with morphological (and physiological, and hence ecological) characters beyond the extremes allowable for the entities recognized as species, and since these phenomena are manifest in the sunflower populations growing throughout the state, no key enabling recognition and determination of every individual is possible. The key below is based on characters of the species as they are known in Tennessee from the herbarium specimens at the University of Tennessee[5] and field observations by the author.

Each of the county records indicated on the county distribution maps (Figs. 2-4) is supported by one or more collections residing in the University of Tennessee herbarium. Records based on specimens in other herbaria are indicated by the appropriate herbarium designation; these have been referred to only in the cases where no specimens from the county are among the University of Tennessee collection. Records of specimens at Indiana University, Missouri Botanical Garden, and Michigan State University are available through the courtesy of Charles B. Heiser, Jr.

A number of collections in the University of Tennessee herbarium are not indicated on the distribution maps because of the uncertainty of the epithets which should be attached to them (collections of apparent hybrids or hybrid derivatives). Except in certain cases *(H. atrorubens, H. silphioides, H. eggertii,* and one collection of *H. microcephalus),* collections of putative hybrids have been omitted from the distribution maps; in those omitted, collections of both of the inferred parental species are represented on the appropriate maps.

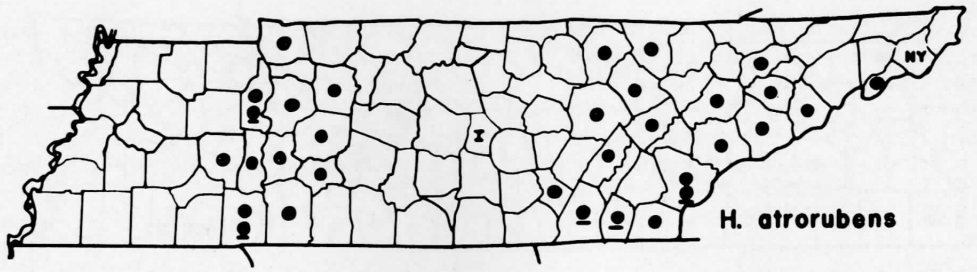
Artificial Key to the Species of Helianthus in Tennessee

1. Involucral bracts broad, firm, appressed, imbricated, glabrous or glabrous except for ciliolate margins, tips obtuse or acute, never long-attenuate.

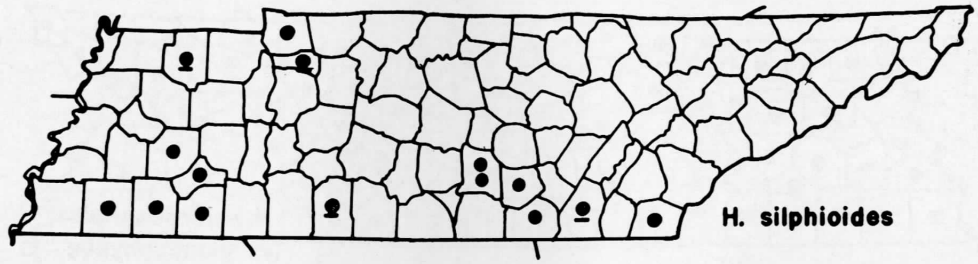
    2. Stems leafy to the inflorescence, the leaves scarcely smaller upward; median and lower leaves commonly dead at flowering times; blades tapering gradually to short petioles, lanceolate to ovate; inflorescence usually consisting of 3 main branches; involucral bracts acute, ovate-lanceolate; disk corollas yellow or less commonly purple; cultivated and escaped.
    (2) **H. laetiflorus**

    2. Leaves chiefly at the lower nodes, long-petioled, conspicuously and often abruptly reduced above; blades oval to broadly ovate or suborbicular, abruptly narrowed to petioles more or less broadly-winged above; involucral bracts oblong-ovate, with blunt to rounded tips (bracts **Silphium**-like); inflorescence alternate-branched; disk corollas purple; native. 3.

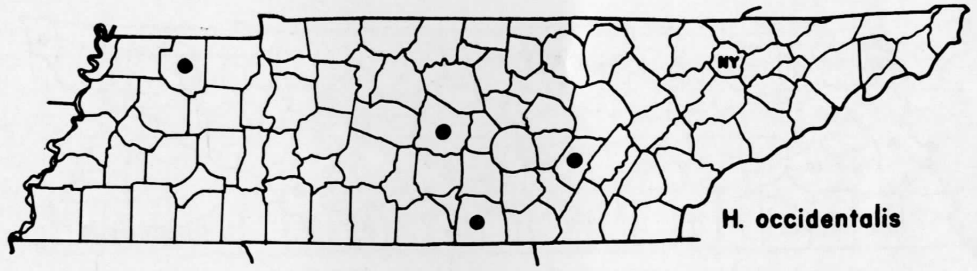
5 These specimens consist of collections made since 1934, at which time the University of Tennessee herbarium was destroyed by fire. This loss was especially regrettable since the herbarium at that time contained the personal herbarium of Dr. Augustin Gattinger, which he had turned over to the University of Tennessee in 1890 and which he characterized as being "the second largest herbarium in the South" (10). Dr. Gattinger's collections of the vascular flora of Tennessee, which began at the time of his emigration from Germany in 1849 as a young man and continued until he was well advanced in years, were the major pioneer botanical effort in the state. Actual number of the Gattinger **Helianthus** specimens and number of species represented are unknown; duplicates of a few of the collections reside in eastern herbaria.



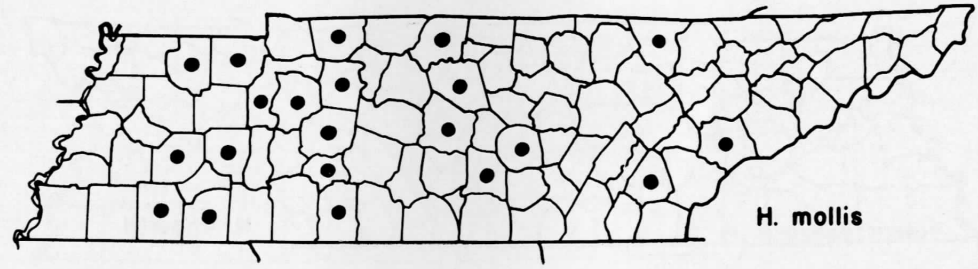
H. atrorubens



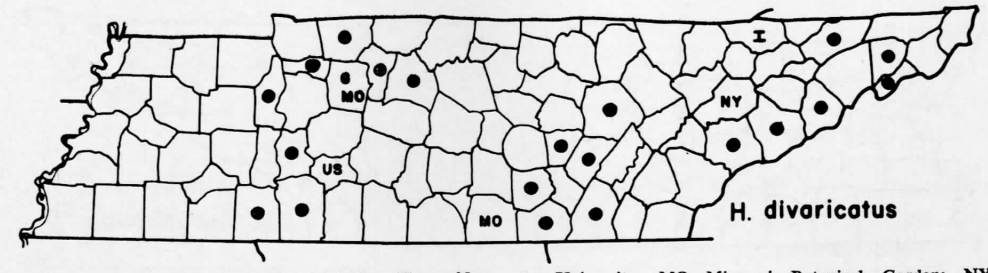
H. silphioides



H. occidentalis

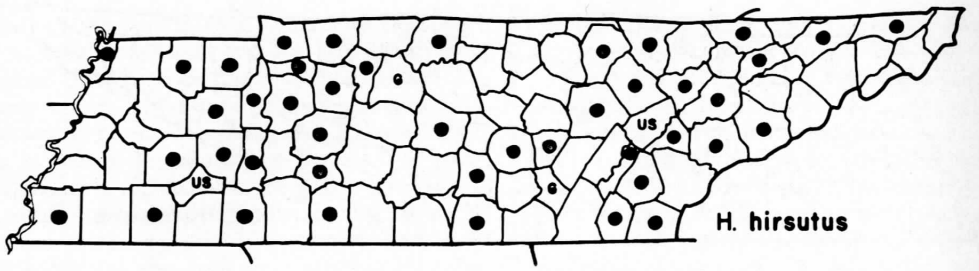


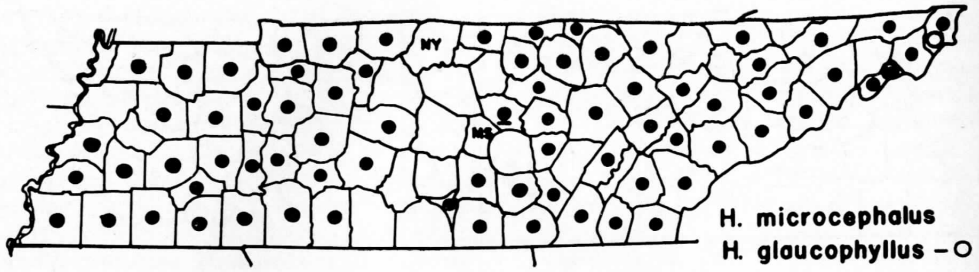
H. mollis

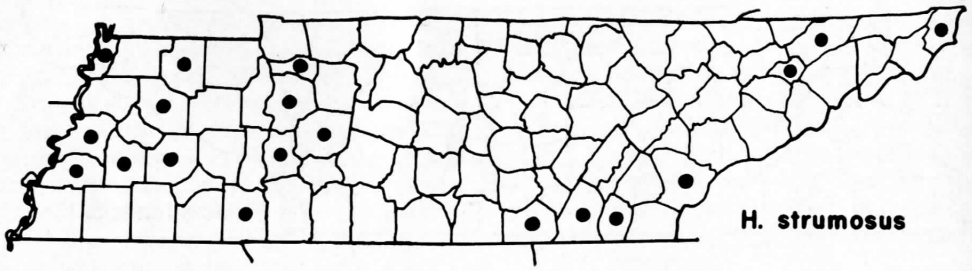


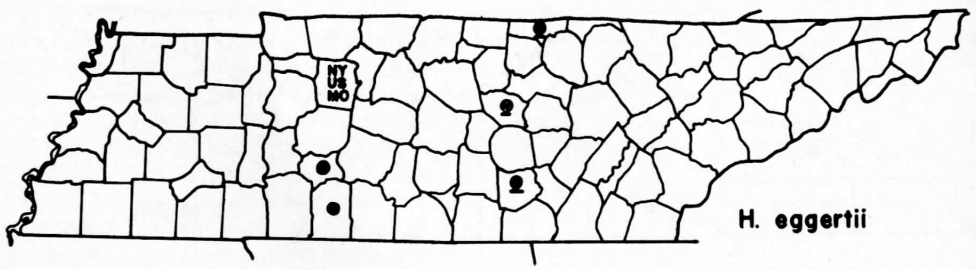
H. divaricatus

Fig. 2. Distribution of **Helianthus atrobens, H. silphioides, H. occidentalis, H. mollis,** and **H. diviarcatus** in Tennessee. Each dot represents one or more herbarium specimens (from a county) which are on file in the University of Tennessee herbarium. Records based on specimens in other herbaria are indicated by letters: I—Indiana University; MO—Missouri Botanical Garden; NY—New York Botanical Garden; US—U. S. National Herbarium. Dots with a line under them refer to hybrids of **H. atrorubens** and **H. silphioides.**









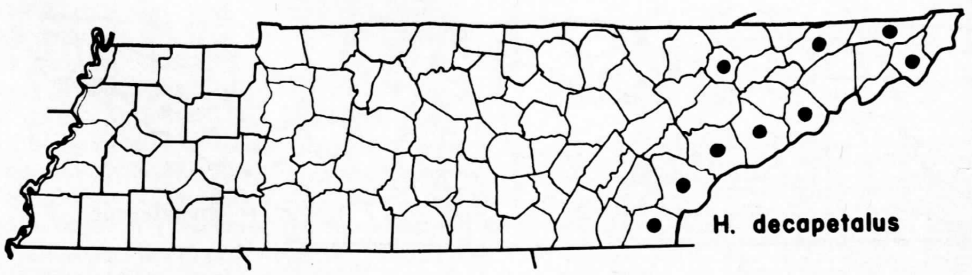
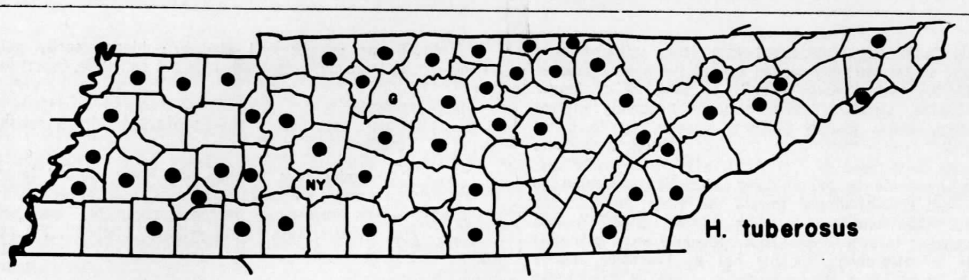
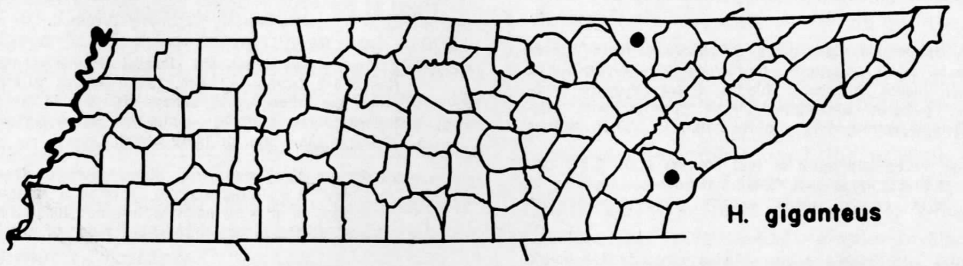
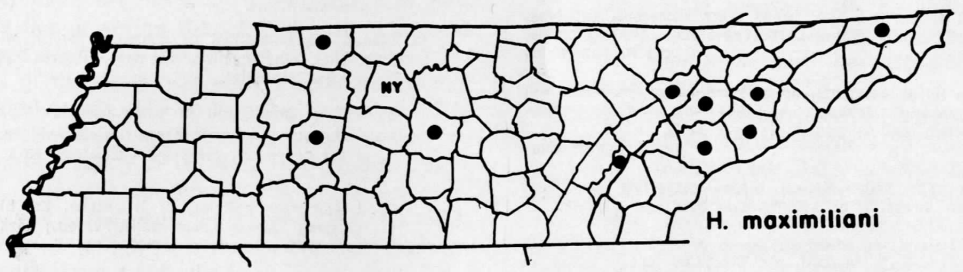
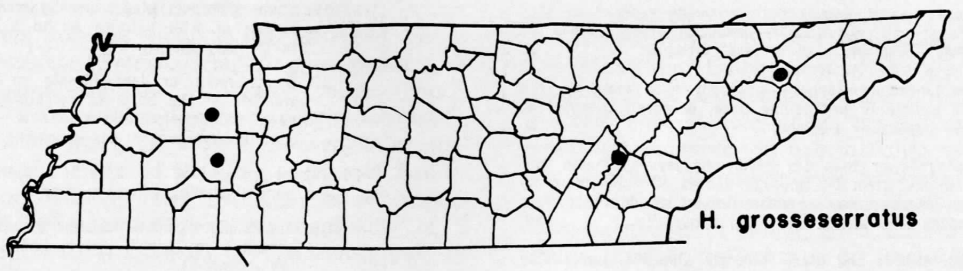


Fig. 3. Distribution of **Helianthus hirsutus, H. mircocephalus, H. glaucophyllus, H. strumosus, H. eggertii,** and **H. decapetalus** in Tennessee. Each dot represents one or more herbarium specimens (from a county) which are on file in the University of Tennessee herbarium. Records based on specimens in other herbaria are indicated by letters: G—Gray Herbarium; MO—Missouri Botanical Garden; MS—Michigan State University; NY—New York Botanical Garden; US—U. S. National Herbarium. Dots with lines under them refer to hybrids.









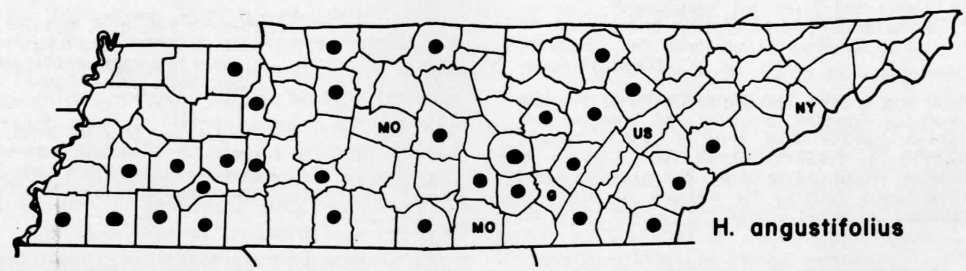


Fig. 4. Distribution of **Heilanthus tuberosus, H. giganteus, H. maximiliani, H. grosseserratus,** and **H. angustifolius** in Tennessee. Each dot represents one or more herbarium specimens (from a county) which are on file in the University of Tennessee herbarium. Records based on specimens in other herbaria are indicated by letters: G—Gray Herbarium; MO-Missouri Botanical Garden; NY—New York Botanical Garden; US—U. S. National Herbarium.

3. Blades oval to oblong, contracted into long, villous-hirsute petioles more or less broadly-winged toward the blade, petioles of at least the lower leaves usually as long as or longer than the blades, slender; leaves abruptly becoming distant and bract-like; stems usually solitary, slender, up to about 2 m. high. (3) **H. atrorubens**

3. Blades broadly ovate to suborbicular, abruptly contracted to petioles always broadly-winged toward the blade, the petioles usually less than one-half as long as the blade; leaves markedly reduced in size upward, but commonly more gradually so than in **H. atrorubens,** usually not as bract-like; stems usually 2 or more, stout, 2-3 m. high. (4) **H. silphioides**

1. Involucral bracts lanceolate (ovate in **H. annuus**), all or at least the inner free at the acuminate or long-attenuate spreading tips, usually more or less hirsute or hispid on the back (essentially glabrous in two spp.). 4.

4. Plants annual; receptacle flat; disks 3-5 cm. or more broad; involucral bracts ovate, abruptly narrowed to the spreading acuminate tips; leaves alternate, blades triangular-ovate, sub-cordate-cordate, petioles unmargined; disk corollas with red-purple (occasionally yellow) lobes; cultivated. (1) **H. annuus**

4. Plants perennial; receptacle more or less convex; disks 0.5-3 cm. broad; involucral bracts lanceolate (often narrowly so) tapering to their apices; disk corolla lobes usually yellow, sometimes purple. 5.

5. Disk corollas with purple lobes; blades narrowly lanceolate to linear (up to 1 cm. broad, usually much narrower), at least 10 times longer than broad, long-attenuate, 1-veined, sometimes revolute. 6.

6. Blades linear, 1-3 mm. broad, very numerous, drooping, crowded, nearly glabrous, not revolute; stems glabrous; cultivated. (20) **H. Salicifolius**

6. Blades linear-lanceolate, up to 1 cm. broad, numerous but not appearing crowded, scabrous above; stems rough-pubescent; native, usually in wet soils. (19) **H. angustifolius**

5. Disk corollas with yellow lobes; blades lanceolate to ovate, more than 2 cm. broad, 1- or 3-veined near base, not revolute. 7.

7. Leaves 3-7 pairs, on lower ⅓ to ½ of stem, blades ovate to oblong-lanceolate, distant and bract-like above, entire or obscurely-toothed; outer involucral bracts with acute to acuminate tips, appressed, inner bracts long-attenuate and spreading. (5) **H. occidentalis**

7. Nodes more than 7, leaves only gradually reduced in size toward the summit, not distant; involucral bracts usually all long-tapering, loose and more or less spreading. 8.

8. Blades lanceolate, tapering gradually to a more or less winged petiole or petiole-like base, obscurely 3-veined at base or apparently 1-veined. 9.

9. Nodes fewer than 15; stem and leaves smooth and glabrous, stem 1-2 m. high, leaves all opposite up to the inflorescence, subentire; disks 1-1.5 cm. broad, rays mostly less than 2 cm. long; native. 10.

10. Leaves and stems strongly glaucous, under side of the blades white or nearly so; stems strongly colonial; endemic of "Oak Barrens" of Highland Rim. (12) **H. eggertii**

10. Leaves and stems not conspicuously glaucous; stems solitary; to be expected at the middle to higher elevations of mountains, East Tennessee. (18) **H. laevigatus**

9. Nodes usually more than 20; leaves mostly alternate (rarely all opposite), numerous and more or less crowded, scabrous above, green or glaucous beneath, subentire to distinctly toothed; stems smooth or scabrous, mostly 2-4 m. high; disk averaging about 2 cm. broad, most of the rays 2-3 cm. long; occasionally introduced species. 11.

11. Stems smooth and glaucous; blades softly pubescent beneath, conspicuously toothed; rays 3-4 cm. long, bright yellow. (17) **H. grosseserratus**

11. Stems scabrous or short-pubescent; blades subentire to distinctly toothed. 12

12. Blades (esp. median and lower) folded lengthwise (conduplicate), the acuminate tips arcuate-recurving (falcate) heads of uppermost branches commonly shortpeduncled to subsessile; rays bright yellow, "cupped", 2-4 cm. long. (16) **H. maximiliani**

12. Blades flat, the acuminate tips not arcurving, heads on long peduncles; rays pale yellow, flat, around 2 cm. long. (15) **H. giganteus**

8. Blades of the ovate-lanceolate type, abruptly contracted into a rounded, truncate, or cordate base, distinctly 3-veined. 13.

13. Blades of at least the largest leaves conspicuously toothed (teeth 1-2 (rarely—6) mm. long); leaves alternate, or opposite below the inflorescence, always alternate in the alternate-branched inflorescence, abruptly contracted to a petiole broadly-winged above; disks 1 cm. or more broad. 14.

14. Blades thick and firm, stems more or less rough-pubescent below the inflorescence; involucral bracts not exceeding height of disk, acuminate but not long-attenuate; floodplains and stream banks throughout most of the state. (14) **H. tuberosus**

14. Blades thin to membranaceous, stems glabrous below inflorescence; involucral bracts long-attenuate, some of them exceeding height of disk; middle and lower elevations in the mountains. (13) **H. decapetalus**

13. Blades shallow-toothed or subentire, or, if with teeth, 2 mm. long, then otherwise not as above; leaves opposite (sometimes upper ones alternate). 15.

15. Blades sessile, all or some cordate-clasping; stem, leaves, and involucral bracts densely whitish-villous; heads showy, on erect peduncles, disks 2-3 cm. broad, rays up to 30. (6) **H. mollis**

15. Leaves with petioles, or if sessile, the blades not cordate-clasping; plants never whitish-villous; disks 1-2 cm. broad, rays 5-20. 16.

16. Blades truncate or abruptly rounded at the base into unmargined petioles less than 2 cm. long, or sessile; leaves horizontally divergent to sub-ascending. 17.

17. Stems glabrous; blades usually truncate at the base, sessile or with petioles up to 5 mm. long; leaves horizontally divergent. (7) **H. divaricatus**

17. Stems more or less hirsute or scabrous; blades truncate at the base, or sometimes (esp. the upper ones) rounded; petioles 0.5-2 cm. long; leaves horizontally divergent or sub-ascending. (8) **H. hirsutus**

16. Blades rounded at the base into petioles more than 2 cm. long (including winged portion). 18.

18. Blades glabrous and strongly glaucous beneath; disks around 1 cm. broad; middle and upper elevations in the mountains. (10) **H. glaucophyllus**

18. Blades more or less pubescent beneath, sometimes glaucous but not strongly so; general distribution. 19.

19. Disks 5-9 mm. broad, rays 5-8; stems smooth and glabrous, often glaucous; main inflorescence branches from upper, middle, and sometimes, lower nodes; heads many; common in most parts of state. (9) **H. microcephalus**

19. Disks 1 cm. or more broad, rays 8-15; stems smooth or sometimes scabrous and sometimes glaucous; inflorescence branches usually from upper nodes only; heads several; uncommon. (11) **H. strumosus**

(1) *Helianthus annuus* L. Field characters: (1) Heads large and showy, disks 3-5 or more cm. broad, disk corollas purple (rarely yellow); (2) leaves alternate, triangular-ovate, dentate, long-petioled, the petioles mostly unmargined; (3) involucral bracts broadly ovate, somewhat appressed except for the spreading abruptly-attenuate tips, margins conspicuously long-ciliate; (4) on or near cultivated grounds only. Flowering July-September.

This is the only annual sunflower known in the state, and it is the "Common Sunflower" which is cultivated in probably every county. Most of the cultivated individuals are of the monocephalic type, each with a single very large head. Also occurring in and around cultivated grounds are plants which resemble the "wild type" of the prairie and plains states, *i.e.,* leaves are smaller and stems are shorter, plants are more or less highly-branched, with several to many heads, and disks are about 3 cm. wide. All in Tennessee appear to be restricted to cultivated grounds, and only uncommonly do individuals occur sufficiently far from human habitations to be considered "escapes."

The closely related western annual species, *H. petiolaris* Nutt., also may occur occasionally in the state although there are no known collections in herbaria. It is earlier flowering than *H. annuus* (12), and is distinguished from *H. annuus* by its white-bearded central bracts of the receptacle and lanceolate, scarcely ciliate involucral bracts (11). According to Heiser (12), if the two species are growing in the same locale, "In general, *H. annuus* seems to be more restricted to heavy soils and *H. petiolaris* to sandy soils . . . [and] *H. petiolaris* is more frequent as a weed of railroads [while] *H. annuus is* more common in waste places about cities and along roadsides."

(2) *Helianthus laetiflorus* Pers. Field characters: (1) Involucral bracts ovate-lanceolate, appressed, acute, glabrous except for the ciliolate margins; (2) leaves opposite, lanceolate, 3-veined, tapering to petioles or petiole-like bases, toothed or nearly entire, upper, median and lower leaves tending to be nearly uniform in size or at least not markedly reduced above, the median and lower usually dead and abscising at time of flowering; (3) stems usually 1-1.5 m. high, more or less scabrous; (4) inflorescence regularly consisting of 3 branches, outer two from axils of uppermost pair of leaves; (5) heads showy, several, disks usually yellow, sometimes purple, 1-2 cm. broad, rays 15-20, bright yellow, 2-3 cm. long; (6) usually restricted to cultivated grounds. Flowering August-September.

This is a widely cultivated sunflower, easily distinguished by its involucral bracts which are unlike those of any other species of *Helianthus* it may resemble in other respects. In most parts of the state it is confined, or essentially so, to its grounds of cultivation. However, in parts of Weakley, Henry, and Stewart counties, this is often the only sunflower on the landscape, and it occurs so frequently in roadside depressions and other open sites more or less away from human habitations, that it is suspected of being a native species in this part of Tennessee. Further studies will be necessary to clarify its status in this area.

The species is reported to be hexaploid (14).

(3) *Helianthus atrorubens* L. (Fig. 2). Field characters: (1) Plants with a scapose appearance—leaves several pairs at the lower nodes, distant and brack-like above; (2) involucral bracts appressed, ovate-oblong, obtuse, and essentially glabrous, resembling bracts of *Silphium;* (3) disks purple; (4) blades oval ovate, or oblong, at least the larger ones distinctly longer than broad, abruptly contracted into a long petiole, the petioles (including the winged portion) of at least the lower leaves as long as or longer than the blade and winged above, the winged portion long-tapering toward the villous-hirsute petiole base; (5) stems slender, characteristically solitary, rarely over 2 m. high, villous-hirsute on at least the lower internodes. Flowering in August and September, with the peak in early September.

This and the following species *(H. silphioides)* are quite distinct from any of the other sunflowers in Tennessee, their closest relative in the state appearing to be *H. occidentalis,* with which they share the scapose aspect and relatively long-petioled leaves. In several respects *H. atrorubens* and *H. silphioides* more closely resemble certain members of the genus *Silphium* than other species of *Helianthus* and may be easily confused with the *Silphiums* until the distinguishing characters are known (see page 137).

Both species are restricted to regions of acid soils in the state, along forest borders in the mountains and especially in the "Oak Barrens" and Oak-Hickory and Oak-Pine forests of the Cumberland Pleateau, Highland Rim, and southern Mississippi Embayment. *H. atrorubens* is a southeastern species, the western margin of whose range in Tennessee lies in the southeastern Mississippi Embayment area (Fig. 1); *H. silphioides* is a species of central United States, the eastern margin of whose range at this latitude nearly coincides with the eastern escarpment of the Cumberland Plateau. Between the Mississippi Embayment of the western part of the state and the Cumberland Plateau escarpment in the eastern part, where their ranges overlap, there is abundant evidence of hybridization and introgression. So common are intergrades between the species that identification of any given individual in a population is often a matter of doubt, or a determination as either one species or the other is an impossibility. Without a knowledge that these occur in a region of overlapping ranges and that the species are interfertile, the *H. atrorubens-H. silphioides* complex would appear to be a single polymorphic species throughout most of the state.

Both *H. atrorubens* and *H. silphioides* hybridize with *H. mollis* in Tennessee (see discussion of *H. mollis*) and may occur on the same sites as *H. mollis, H. microcephalus, H. hirsutus, H. divaricatus;* in the southeastern Coastal Plain Uplands *H. silphioides* sometimes grows with *H. angustifolius.* Putative hybrids of *H. atrorubens* and *H. angustifolius* have been reported by Martin (23), but these, or crosses of *H. angustifolius* with *H. silphioides,* would not be expected to occur commonly in Tennessee since *H. angustifolius* is

ordinarily ecologically separated from the others; geographically, however, the distribution of *H. angustifolius* closely parallels that of *H. atrorubens* and/or *H. silphioides* throughout the state.

Both *H. atrorubens* and *H. silphioides* are diploids (14).

(4) *Helianthus silphioides* Nutt. (Fig. 2). Similar to *H. atrorubens,* but distinguished by the following: (1) Leaves markedly reduced in size above and internodes conspicuously longer above, but leaves not as bract-like nor as remote as in *H. atrorubens;* (2) blades large, thick and coarse, broadly ovate to suborbicular, abruptly contracted to a petiole broadly-winged above, the longest petioles (including the winged portion) usually less than one-half the length of the blade; (3) stems typically 2-3 m. high, stout, scabrous-pubescent, usually colonial. This is generally a much more robust plant than *H. atrorubens.* Flowering time as in *H. atrorubens.*

See discussion of *H. atrorubens.*

(5) *Helianthus occidentalis* Riddell (Fig. 2). Field characters: (1) Stems rough-pubescent, in Tennessee specimens solitary and usually less than 1 m. high; (2) leaves several pairs at the lower nodes, opposite, distant and bract-like above, blades ovate-lanceolate or oval, acute or obtuse, entire or minutely-toothed, pubescent above and below, abruptly contracted to a petiole winged near the base of the blade, the petioles longer than the blade (often much longer) in the lowermost (largest) leaves; (3) disk yellow, about 1 cm. broad, rays 1-2 cm. long, bright yellow; (4) involucral bracts lanceolate, acuminate-attenuate, at least the inner loose and spreading. Reported by Watson (33) as "almost always producing a flat rosette of leaves toward the end of the season" (see footnote 3). Flowering August-September.

Helianthus occidentalis is apparently either a rare native species in Tennessee, or only rarely has been introduced into the state. It has a broad geographical range (Minnesota to Ohio, south to Florida and Texas (8)), and although Tennessee lies toward the center of its latitudinal range, there are but six collections known from the state; these are from five scattered counties. Smith and Martin (32) describe it as "a common plant of the prairies and sand hills of the midwest from Michigan to Texas and [it] is occasionally encountered in the Southeast." It was not cited by Gattinger (9, 10) as a Tennessee species in 1887 or 1901.

Naturally-occurring hybrids of *H. occidentalis* and *H. mollis* are reported by Jackson and Guard (16) to occur generally in the areas of Indiana where the two species grow together. The hybrid populations are reported to vary from several to over 1,000 individuals. They are known also from three other states. The species is reported also by these same investigators to hybridize naturally with *H. grosseserratus* and uncommonly with *H. divaricatus.* Where collected during this study, *H. occidentalis* was associated with open, pioneer or old-field xeric sites of the kind with which *H. mollis* and *H. divaricatus,* which are among the commoner sunflowers of the state, may be associated, and on which the rare *H. grosseserratus* also grows. Natural hybridization of *H. occidentalis* with these species may contribute occasionally to local variation in the Tennessee native sunflowers when or if there is opportunity for hybridization.

The species is reported to be diploid (14).

(6) *Helianthus mollis* Lam. (Fig. 2). Field characters: (1) Leaves opposite, triangular-ovate, 3-veined, sessile, more or less cordate-clasping; (2) entire plant densely villous with white hairs; (3) heads large and showy, on long, erect, mostly unbranched peduncles, the heads typically with more ray flowers than any other perennial sunflower, the rays about 2 cm. long, bright yellow, appearing somewhat crowded and overlapping along the disk margin, disk 2-3 cm., broad, yellow; (4) stems 0.5-1 m. high, *i.e.,* short-stemmed compared with most of the sunflowers, often colonial. Flowering July-September, with the peak in August.

This is a very distinct sunflower, which grows on open xeric sites in most parts of the state except in the mountains. It is found especially in the acid soils of the Highland Rim and Coastal Plain Uplands, and in the calcareous soils of the Cedar Glades and Cedar Barrens of the Central Basin and elsewhere. It is sometimes cultivated since it makes an unusually attractive ornamental. The distribution indicated in Fig. 2 probably reflects incomplete collecting of this species because (1) its presence is often obscured by the taller old-field vegetation with which it is frequently associated; (2) it is a midsummer-flowering species at which time it is conspicuous, and the bulk of the species of *Helianthus* collections have been made in late summer and autumn, when its grey-green aspect makes it notably inconspicuous; and (3) it is not an aggressive invader of new areas (though long-persisting once established), and therefore does not commonly occur along roadsides or on other open sites of recent disturbance where it would be more readily visible to collectors.

Helianthus mollis frequently grows in Tennessee on the same sites as *H. silphioides* and *H. atrorubens,* and wherever they grow together putative hybrids may be expected. One such population was noted in the "barrens" country of Lewis County (*Beatley,* UT 26616-18, 1959); this consisted of one large colony of *H. mollis,* 4 individuals of *H. atrorubens,* and 5 putative hybrids, all growing in about a 10-foot square area 100 yards or so from any other individuals of these (or other *Helianthus*) species. At this time (September 7), *H. atrorubens* was at the peak of its flowering, but flowering in the colony of *H. mollis* was essentially past. The *H. atrorubens* plants were about 1.5 m. tall, and the stems of *H. mollis* were scarcely 0.5 m. tall.

Within this small hybrid population there is rather great variability with regard to the combination of characters expressed in any one plant. There are purple disks with relatively many rays, and yellow disks with relatively few rays; the inflorescence varies from a single erect, rather stout peduncle, to one alternate- and slender-branched; stem length is variable but interme-

diate between that of the parents; pubescence, though variable, more closely approaches that of *H. atrorubens* in all cases; leaf shape is generally what might be anticipated as an intermediate condition between that of blades abruptly contracted to long, winged petioles, and that of cordate-clasping leaves—blades from their broadest point abruptly taper to relatively short petiole-like bases; leaves are mostly conspicuously reduced in size at the upper nodes, but none has the pronounced scapose aspect of *H. atrorubens;* involucral bracts are mostly ovate and acute, are somewhat pubescent on their outer surfaces, and some of the bracts are loose and spreading; all were past their flowering peaks when collected, but among the group there were yet some relatively young heads. None of these putative hybrids could be referred to as being vigorous, and pollen stainability counts in the three individuals taken for herbarium specimens were 26, 33, and 45 percent.

Two specimens (*Beatley,* McNairy Co., UT 26676, 1959, and Sharp & Sharp, Coffee Co., UT 22614, 1957) appear to be hybrids or hybrid derivatives of *H. mollis* and *H. silphioides* (det. by C. B. Heiser, Jr.). Leaves are shaped and disposed much like those described above, pubescence is less dense than in *H. mollis* and scarcely of the white-villous type, disks are yellow, and the involucral bracts are long-attenuate and relatively narrow as in *H. mollis.*

Jackson and Guard (18) were able to cross *H. mollis* with *H atrorubens* (both diploid species) experimentally, and their F_1 hybrid was described as "vigorous" though partially sterile. The species were considered interfertile on the basis of this cross, and a mechanism "tend[ing] to keep . . . these species separated" was suggested to be their general spatial isolation, "with *(H. atrorubens* being) found in the southeastern part of the United States while *(H. mollis)* is mostly a prairie species." That such a mechanism is not operating in Tennessee, where *H. atrorubens* is at the northwestern margin of its range and, like *H. mollis,* occurs throughout most of the state, is evident, particularly in regions where both species and/or *H. silphioides* grow rather commonly on the same sites. Additional field observations in these regions will probably substantiate the belief that hybrid swarms, such as described above, are of not uncommon occurrence in certain areas of the state.

Helianthus mollis has been reported by Jackson and Guard (17, 24) to hybridize naturally with *H. divaricatus, H. grosseserratus,* and *H. giganteus* (the hybrid being known previously as *H. doronicoides* Lam. (15), Jackson and Guard (18) reported it to hybridize also with *H. occidentalis.* Of these, *H. mollis* x *H. divaricatus* is the most likely to occur in Tennessee sunflower populations, and where the two species are growing on the same or contiguous sites, as may often be the case, hybrid swarms can be expected in which the hybrids will predictably be more or less intermediate between the parental species. Flowering in *H. divaricatus* begins earlier (late June) than does that of *H. mollis* (late July), but their flowering periods overlap in Tennessee. Natural hybridization of the other species with which interfertility with *H. mollis* has been demonstrated, although possible, is unlikely to occur because of the rarity of occurrence of all of these species in the state.

(7) *Helianthus divaricatus* L. (Fig. 2). Field characters: (1) Leaves strictly opposite, triangular-ovate, typically truncate but sometimes broadly rounded at the base, sessile or nearly so (petioles less than 0.5 cm. long) but never cordate-clasping, strongly divaricate, margins subentire to obscurely-toothed, 3-veined, scabrous above, more or less pubescent beneath; (2) stems rather slender, glabrous, sometimes glaucous, 0.5-1 m. high; (3) heads few, disks yellow, about 1 cm. broad, rays 8-15. This is the earliest-flowering sunflower in the state (late June or early July to mid-August), the latter part of flowering overlapping more or less with that of most other perennial sunflowers.

Helianthus divaricatus is a species primarily of xeric upland forest borders or open woodlands, occurring less commonly in old fields or other open, abandoned, xeric sites, and even less commonly along roadsides or on similar disturbed sites. Perhaps the species is more common than collections to date appear to indicate, for the same reasons a similar statement is believed to be true of *H. mollis* (see discussion of *H. mollis*).

The species has been reported by Smith and Guard (31) to hybridize naturally, and with some difficulty following artificial crossing, with *H. microcephalus,* resulting in more or less fertile F_1 plants. Hybrid swarms studied by these investigators were in Indiana, but "additional hybrid swarms have been discovered in Kentucky, Tennessee, and North Carolina"; presumably one such is that indicated on their distribution map (Fig. 10, Smith and Guard (31)) in Hamilton County, Tennessee. Of their discussion of hybridization of these species, the following is pertinent to the occurrence of these hybrids in Tennessee:

> In studying populations of these species . . . all the hybrid swarms have occurred in disturbed areas. The usual place . . . is a cut-over woodland, either along, or near a road . . . which is in line with Anderson's hypothesis . . . that in order for introgression to occur, there must be a 'hybridization of the habitat.' Thus, it appears that the chief isolating mechanisms separating these two species are ecological rather than genetic. Since both the species . . . are perennials, removal of the forest cover does not necessarily remove them from the area. Quite the contrary, in fact, in the case of *H. divaricatus,* which seems to grow much more vigorously when the competition of trees is removed. One result of the increase in vigor is that the plant branches much more than normal, and more capitula are produced, thus effectively lengthening its period of blooming. This is quite important, since *H. microcephalus* normally does not come into bloom until *H. divaricatus* has ceased flowering. However, with this extension of the flowering period of *H. divaricatus,* their periods of anthesis overlap, permitting hybridization to take place. One additional . . . barrier to hybridization [is that since] artificial hybrids are difficult to obtain . . . this same factor **[may be] operative in** nature, which would effectively retard hybridization. . . . Hybridization seems to have had little effect upon the immediate populations of the two parental species outside of the areas where active crossing is occurring [and] introgression appears to be extremely localized.

Although these authors consider that there is generally a significant degree of ecological (and geographical) isolation between *H. divaricatus* and *H.*

microcephalus, this would scarcely hold for populations in Tennessee, where the species may occur on the same sites. "Hybrid habitats" would, therefore, not be a necessary accompaniment to the growth and persistence of hybrids or to introgression between these species, since this would be true only in cases where hybridizing species are ecologically distinct. Flowering times also generally overlap in Tennessee, with *H. microcephalus* beginning its flowering at a time well past the flowering peak of *H. divaricatus,* but with sufficient overlap that possibility of crossing would not be excluded on this basis alone. The occurrence of such hybrids, insofar as genetic mechanisms of the parental species permit, can be expected not uncommonly, particularly in the western Highland Rim and southern Cumberland Plateau, where both species are more or less well represented in and characteristic of the open forests and forest borders of the xeric uplands.

Hybrids of *H. divaricatus* and *H. microcephalus* are believed by Smith and Guard (31) to be what has been referred to *H. glaucus* Small in the past, and it is suggested that "certain of the natural polyploids, such as *H. decapetalus* and *H. strumosus,* resemble hybrid derivatives of *H. divaricatus* and *H. microcephalus,* and could conceivably have been the parents of one or more of the polyploids."

Helianthus divaricatus has been reported to hybridize naturally also with *H. mollis* (16, 18), resulting in partially sterile F_1 hybrids. As in *H. divaricatus* x *H. microcephalus,* the presence of a "hybrid habitat" is implied to be a factor contributing to the presence of these Indiana hybrid populations. In Tennessee, however, these two species may be expected to occur on the same sites, although perhaps less frequently than in the case of *H. divaricatus* and *H. microcephalus,* since *H. mollis* is primarily a species of open sites rather than forest borders or open forest types. Ecological separation, though, cannot be considered a potentially significant barrier to hybridization in this state. Hybrids, of course, could be expected to occur also, as in Indiana, in habitats which are "hybrid" with respect to those of local populations of the parental species.

Smith and Guard (31) point out that *H. divaricatus* "is to be found in Arkansas, Missouri, and Oklahoma . . . [and that] this range either parallels or overlaps at one point or another the ranges of all but the far western species of *Helianthus.* Consequently, numerous opportunities for hybridization with many species exist, and a large number of putative hybrids have been reported and collected." It is likely, then, that hybrid swarms resulting from crosses of *H. divaricatus* with a number of other species of *Helianthus* can be expected in the Tennessee sunflower populations.

It appears worthy of note that close inspection of *H. hirsutus* populations in Tennessee sometimes reveals scattered individuals with smooth and glabrous stems which, as herbarium specimens, would be referable to *H. divaricatus.* Likewise, individuals with scabrous stems, and otherwise referable to *H. hirsutus,* occur in *H. divaricatus* populations. Moreover, individual members of a basically *H. divaricatus* population may exhibit sufficient variation that some may be referred to *H. strumosus* (leaf blades rounded at the base into petioles much longer than the usual *H. divaricatus*). That three different epithets may be attached to members of a single population (*Shaver* 2795, Dickson Co., UT, 1942) when each is viewed independently of other members of the population is likely a manifestation of introgression from other species.

(8) *Helianthus hirsutus* Raf. (Fig. 3). Field characters: (1) Stems rough-pubescent or scabrous, rarely over 1 m. high, usually solitary; (2) leaves usually all opposite, divaricate to subascending, 3-veined, obscurely-toothed, blades highly variable in shape and density of pubescence, from triangular-ovate with a broad truncate base to (less commonly) lanceolate and a rounded base, rough-hispid above and beneath, always evidently petioled, the petioles 0.5-1.5 (—2) cm. long, unmargined or nearly so; (3) heads few, disks yellow, 1-2 cm. broad, rays 1-2 cm. long, bright yellow. This is a midsummer-flowering species (July and August, continuing into September in some parts of the state); its flowering time overlaps for the most part that of *H. divaricatus,* and to a lesser extent that of most other perennial sunflowers in Tennessee.

This is apparently a "good" southeastern species, and perhaps in no other state of eastern United States is it better represented geographically or by numbers of individuals than in Tennessee, where soils and climate appear to be optimum for the species. It is the second most abundant sunflower in the state, occurring in most counties in greater or lesser numbers. From what has been observed of its distribution to the present time, *H. hirsutus* grows in greatest abundance in the acid soils associated with the "Oak Barrens" or open Oak-Hickory and Oak-Pine forests of the Cumberland Plateau, the southeastern and certain parts of the southwestern Highland Rim, and the southeastern Mississippi Embayment, but it is associated also with the calcareous soils of the Cedar Glades and Cedar Barrens in the Central Basin and with such soils elsewhere, as in the Appalachian Valley (Fig. 1).

It is a species of xerophytic forest or successional vegetation and is tolerant of partial shade, but occurs as frequently in the open, especially in upland old fields, and along roadsides and fence rows. It may grow on the same sites as *H. microcephalus, H. divaricatus, H. mollis, H. silphioides,* and *H. atrorubens.* It appears to be an even more "aggressive" sunflower than *H. microcephalus,* the state's most abundant and widely distributed species of *Helianthus;* it is likely that this is because *H. hirsutus* can grow on a rather great variety of sites from which *H. microcephalus* is excluded by its usual requirement of partial shade. In its ability to invade upland pioneer sites and to persist through various stages of secondary succession, it ranks first among the sunflowers of the state.

Helianthus hirsutus is a highly polymorphic species, unsurpassed among the species of *Helianthus* in Tennessee for its great variability in morphological characters. The two varieties and typical *H. hirsutus* recognized by Fernald (8) all occur in the state without

geographic definition or habitat distinction. Watson (33) states: ". . . as I have observed this species throughout its range, it is almost impossible to find two plants that closely resemble each other", and this would be an entirely accurate description of the Tennessee populations in themselves. Variation in size and shape of leaves and height and vigor of plants growing side by side may include the extremes of all leaf, stem, and inflorescence characters.

The degree of morphogenetic variability in *H. hirsutus* is comparable to that in *H. strumosus* (see discussion of *H. strumosus*). Like *H. strumosus* in part, *H. hirsutus* is a tetraploid species (counts based on Indiana and Kentucky specimens (14)), and it appears, on the basis of morphological criteria, that there is a close genetic relationship with *H. divaricatus*. In populations of *H. hirsutus* in Tennessee there occur occasional individuals with smooth stems and nearly sessile leaves which would be referable to *H. divaricatus* under other circumstances.

No reports of natural hybridization of *H. hirsutus* with other species are recorded in the published literature. One collection (steep roadside embankment, *Beatley*, Knox Co., UT 26637, 1959) appears to be a hybrid swarm, or hybrid derivatives, of *H. hirsutus* x *H. tuberosus*. These individuals vary from short *hirsutus*-like plants to tall and extremely robust forms. All have thick and firm more or less divaricate opposite leaves, with leaf characters variously intermediate, including especially an abrupt contraction of the blade into a broadly-winged short petiole. Rays of most plants are orange-yellow as in *H. tuberosus*, and time of flowering (mid-September) is that of this species also. The over-all field aspect of this population was one of intermediacy between these two species, including the habitat in which they were growing.

(9) *Helianthus microcephalus* T. & G. (Fig. 3). Field characters: (1) Small heads, *i.e.*, disks less than 1 cm. broad, heads numerous except in depauperate individuals; (2) rays only 5-8, highly variable in length in a given head or in the heads of a given plant; (3) highly branched form (except when depauperate) in which respect it generally greatly exceeds that of any other sunflower, the branches of the inflorescence arising from axils of median and upper leaves, and sometimes lower leaves as well; (4) stems smooth and glabrous, often glaucous; (5) essentially confined to forest borders or other partially shaded sites throughout most of the state. Leaves are variable, *i.e.*, the blades may be lanceolate to broadly ovate, smooth or scabrous-hispid above, usually tomentose beneath but sometimes sparsely short-pubescent or pubescent on the veins only, margins subentire to distinctly toothed, but in all the blades are rounded at the base into slightly-winged petioles. Flowering August into October, at peak in early September.

The species is without question the most widespread and abundant sunflower in Tennessee. Throughout its range as a whole, Watson (33) characterizes it as being "not very abundant", but Smith and Guard (31) note that it is "a very common species of open woodland in the southeastern states." It occurs in all parts of the state (often in profusion) except in the Central Basin, the dissected Highland Rim, and the inner part of the undissected Highland Rim (as defined by DeSelm (6)). Its distribution is sharply delimited a few miles back of the inner margin of the undissected Rim; and in the Basin-Rim region of the state, where field observations indicate its occurrence could be mapped with precision, the distribution is undoubtedly directly correlated with bedrock, and hence soil properties. The species is most abundant in areas of moderately to strongly acid and sterile soils, such as those derived from sandstones and noncalcareous shales, and appears to be absent only in regions where soils are derived from highly calcareous materials. In this connection, it may be noted that there is essentially perfect correlation between the occurrence of Cedar *(Juniperus virginiana)* as a dominant species and the absence of *H. microcephalus* from the landscape, a relationship so well-defined that it is evident even when distributions are compared on the broad basis of counties (cf. Fig. 3 with stippled area of Fig. 9 in Shanks (24)). In the northern and southern Highland Rim counties it is usually the only sunflower species on the uplands, and in some areas of the northern Highland Rim it is exceedingly abundant.

Helianthus microcephalus is a forest border or open-forest species, only uncommonly growing on sites exposed to full sunlight, and is almost strictly an upland mesophytic and xerophytic species, rarely if ever occurring on floodplain or other sites with imperfect drainage. That it is the most "successful" of our sunflowers appears to be due in part to its ability to grow in soils with a rather wide range of physical and chemical properties, *i.e.*, the species is one of rather great "edaphic amplitude", and the kinds of soils with which it may be associated are heavily represented in all regions of the state except in the Basin-inner Rim area. Its current success is due in part also to the great increase, since European occupancy of the state, of the forest border habitat, as nearly everywhere the habitat occurs, *H. microcephalus* has become established in greater or lesser numbers. Its abundance today cannot be used as an index to its frequency in the vegetation of the state prior to the widespread disturbance of the landscape during the past century and a half, but there can be little doubt that it was originally, as today, a species well represented in the open forests of the uplands, and to a lesser extent in other forest types, and that it is eminently well-adapted to the soils and climate of the state.

The species is reported to hybridize with *H. divaricatus* in Indiana and in "Ky., Tenn. and N. Car." by Smith and Guard (31); such a hybrid (or hybrid population) is reported by these authors from Hamilton County, Tennessee (Fig. 10, p. 143). Naturally-occurring hybrids of *H. microcephalus* and *H. divaricatus*, and perhaps hybrids of *H. microcephalus* and certain other species as well, may be overlooked easily in the field because of the great morphological variability in the Tennessee *H. microcephalus* populations (a characteristic of the species also noted by Watson (33)). Hybrid swarms from these parental species can be ex-

pected in Tennessee since there appears to be no ecological barrier (the two may grow on the same sites), flowering times are at least sometimes overlapping, and the species have been demonstrated by Smith and Guard (29) to be without apparent genetic barriers to hybridization.

From collections made in the present study, *H. microcephalus* is suspected of having hybridized some time in the past with *H. eggertii* on the eastern Highland Rim (see discussion of *H. eggertii*). Smith and Martin (32) report that within a local mixed population of *H. microcephalus, H. occidentalis, H. atrorubens,* and *H. longifolius* in northern Alabama there was no evidence of hybridization of *H. microcephalus.*

(10) *Helianthus glaucophyllus* D. M. Smith (Fig. 3). Distinguished by Smith (29) from *H. microcephalus* by the "glabrous, glaucous lower leaf surface, somewhat larger heads (0.9-1.3 cm.), [and] erect phyllaries" and by its occurrence "at rather high elevations in the Appalachian Mountains." "Moist forests and open shade along roadsides, generally above 2,500 ft., in the Blue Ridge and Smoky Mountains of North Carolina and Tennessee. Flowering in August and September." Smith considers the species "is clearly as distinct from *H. microcephalus* as *H. giganteus* L. and *H. grosseserratus* Martens are from each other, or as *H. strumosus* is from *H. decapetalus* L."

Specimens on which the county records of Fig. 3 are based are those examined by Smith prior to his description of this as a new species *(Underwood & Sharp,* Johnson Co., UT 3136; *Alexander, Everett & Pearson,* Unicoi Co., NY).

(11) *Helianthus strumosus* L. (Fig. 3). Placed in this species are Tennessee sunflowers with the following field characters: (1) Leaves opposite, blades ovate-lanceolate, 3-veined, acuminate, scabrous-hispid to merely scabrous above, more or less pubescent beneath, obscurely-toothed to serrate, abruptly *rounded* at the base into a more or less margined petiole, the petiole usually 2 cm. or more long; (2) stems smooth or scabrous, solitary, 1-2 m. high; (3) inflorescence of few to several main branches, the branches arising from the upper leaf axils, heads several, involucral bracts narrowly lanceolate, attenuate-acuminate, disks 1-1.5 cm. broad, yellow, rays 8-15, 2-3 cm. long, bright or golden-yellow. Flowering in late summer and early autumn.

As described above, this is a species lacking clear definition since the characters are intermediate ones for one section of the genus, and with no characters, morphological or ecological, that can be pointed to as diagnostic. The epithet is one, in fact, to which individuals of quite different aspect and a wide range of characters have been assigned in the Tennessee sunflower populations—in most cases for lack of any other species category in which to place them.

From field observations and collections made throughout the state of Tennessee during this study, the following can be stated with regard to the status of *H. strumosus* as a species in this state. *Helianthus* specimens to which the epithet, *H. strumosus,* has been assigned are of two kinds: (1) Those which are individuals selectively collected from among a local *Helianthus* population because of their unusual morphological characters or aspect, *i.e.,* because they were different from most other members of the population; and (2) individuals from the occasional local populations which occur in nearly any part of the state, almost no two of which would be judged in the field to be populations of the same species, particularly when the populations being compared are from different geographic areas of the state. Such individuals and populations appear to be an expression of genetic diversity and the products of hybridization and introgression within the genus.

It has been concluded in this study of the genus in Tennessee that epithets to be assigned to these individuals and populations, whose morphological characters are within the broad range of those allowable for *H. strumosus,* may be arrived at in three ways: (1) All such plants be relegated to one epithet, *H. strumosus,* but with the understanding that the genetic (and hence morphological, physiological, and ecological) diversity exceeds that normally allowable for a species; (2) each population be considered a different taxon and be described as such; and (3) recognition of the impossibility of placing such individuals or populations in a current taxonomic category, and no effort be made to attach names to them until their genetic constitutions have been studied and understood in relation to the rest of the genus.

Judgments of the best procedure to be followed with regard to the treatment of this very complex problem, or efforts to contribute to its solution, have been beyond the scope of the present study, and hence the current acceptance of *H. strumosus* as a species of eastern United States, even though a "waste-basket" species, has been followed in this study which is concerned with the species of *Helianthus* of one area within that region.

The observations of the character of populations and individuals of *H. strumosus* in Tennessee appear to be confirmatory of the situation which exists and has been recognized elsewhere by others. Watson (33) expressed the problems of recognition of this as a species when he stated: "The precise interpretation of *H. strumosus* is more uncertain than that of any other of our sunflowers, and it is beyond doubt that no specific name has been more generally misapplied than this." Smith (28) (reported in Heiser and Smith (14)) has found both tetraploids and hexaploids in *H. strumosus,* and according to Heiser and Smith (14), "Perhaps the most difficult species from a taxonomic standpoint is *Helianthus strumosus,* which Watson segregated into numerous 'species'. . . . It is now apparent that *H. strumosus* comprises both tetraploid and hexaploid populations which may account for some of the taxonomic difficulties". Smith (personal communication, December, 1959) states that "whether we consider each of its local populations as distinct species—as Watson did—or lump all this under one name seems to be a matter of preference . . . a 'useful' solution seems doubtful."

Because of the exceptional uncertainty of the applicability of this epithet for several collections made during this study, in which the characters fall within the range of those allowable for *H. strumosus* but in which the aspect of the populations from which they came is known to have been manifestly different, certain specimens in the University of Tennessee collection have been excluded from the distribution map in Fig. 3.

(12) *Helianthus decapetalus* L. (Fig. 3). Field characters: (1) Leaves opposite below the inflorescence, alternate in the inflorescence; (2) blades ovate to broadly lanceolate, 3-veined, conspicuously toothed (serrate-dentate), thin and membranaceous, slightly scabrous above, sparsely pubescent to nearly glabrous beneath, acuminate, abruptly contracted to a winged petiole; (3) heads few to several, some of the involucral bracts longer than the disk, very loose and somewhat reflexed at the tips, narrow, attenuate-acuminate, disks 1-2 cm. broad, rays 8-15, bright yellow, 2-3 cm. long; (4) upland mesophytic forests and forest borders of the mountains. Flowering August-September.

The species is here considered to be restricted, or essentially so, to the middle and lower elevations in the mountains of the eastern part of the state, a distribution which is comparable with that of many other species whose centers of distribution lie at more northerly latitudes. It is described by Watson (33) as "found most abundantly in New England, New York, west to Michigan (and Wisconsin), Ohio, Kentucky and Tennessee, occasionally in the States bordering on this range . . .". The species is evidently not a southern one, and its confinement to the mountains of Tennessee, despite herbarium specimens from other parts of the state to which this epithet has been attached (which specimens are not included in Fig. 3), is in accord with the state-wide field observations made during the present study. Individuals which have been selectively collected in other parts of the state, and referred as herbarium specimens to *H. decapetalus* because of the strongly-toothed leaf blades, smooth stems, and very loose involucral bracts, are here considered to be putative hybrids or hybrid derivatives of *H. tuberosus* and other species. Chapman (3) recognized *H. decapetalus* as a species occurring in the "mountains of Georgia, and northward." Gattinger (9) placed it in the "mountains of East Tenn.; Paradise ridge"; later (10) he included also the "Highlands of M[iddle] Tenn.", a conclusion which may have been based upon his observation of individuals resembling those collected in this part of the state in recent years and here inferred to be putative hybrids of other species.

Both tetraploids and diploids have been reported in *H. decapetalus* populations (30).

(13) *Helianthus tuberosus* L. (Fig. 4). Field characters: (1) Floodplain species, or on other soils at least seasonally imperfectly- to poorly-drained, rarely if ever growing on other kinds of sites; (2) leaves usually opposite at the lower nodes and alternate above, sometimes all opposite below the inflorescence, secondary branching and leaves within the inflorescence nearly always alternate; (3) blades large, and at least the largest ones conspicuously toothed (serrate-dentate), the principal blades broadly ovate, abruptly narrowed to a winged petiole; (4) involucral bracts narrow, loose, attenuate-acuminate, mostly not exceeding height of the disk, disks averaging about 2 cm. broad, rays 2-4 cm. long, up to 1 cm. wide, deep orange-yellow. The species is often tuber-bearing, for which it is reputed to have been widely cultivated in the past, but it appears to be seldom cultivated in the state today. Flowering August-September.

This is our only yellow-disk sunflower associated with bottomland or edaphically comparable sites, and it is so closely restricted to such sites that any individuals resembling this species and occurring on the uplands are suspect of being hybrids or hybrid derivatives. In all cases observed in the field, the field aspect and morphological characters of these individuals, occurring sporadically or in small populations, are sufficiently different from the usual *H. tuberosus* to justify this inference. The species is somewhat shade-tolerant, frequently occurring along borders of swamp forests, but is most common on open floodplain sites, stream banks, and roadside ditches or other depressions.

Next to *H. microcephalus,* it is the most widely distributed sunflower in the state. It appears never to be abundant, the local populations consisting of a few to several individuals, but there are relatively few counties along whose streams this species does not occur in greater or lesser numbers. It was not observed in the Central Basin during the field work of this study, although Gattinger reported in 1887 (9) that it was "very frequent around Nashville", and a specimen is on file from a roadside near Murfreesboro, Rutherford County (*DeSelm* 942, UT, 1955). Field observations seem to indicate that it is absent in the Basin itself, but it appears immediately on the landscape of the dissected Highland Rim which surrounds the Basin on all sides, and here appears to be the principal or sole representative of the genus. That it may sometimes occur in the Basin as tongues along the water-courses confluent with those of the surrounding Rim seems probable.

The species also is either absent or rare in the Cumberland Plateau, suggesting that it is intolerant of highly acid soils as well as the highly calcareous soils of the Central Basin. However, physiographic conditions, *i.e.,* the relative infrequency of the floodplain habitat in the Plateau, may be the cause of its apparent absence as inferred from collections to date. The species does occur along streams at least at lower elevations in the mountains though specimens have not been collected in this region. In the Mississippi Embayment of the western part of the state, *H. tuberosus* is not especially common, as might be expected since its lowland habitat is represented over large areas; it is, in fact, inclined to be less frequent here than in the other physiographic areas of the state where it predictably occurs.

In the literature there are frequent statements that the widespread distribution of *H. tuberosus* throughout central and eastern United States is to be attributed to

its widespread cultivation by the aborigines. For example, Watson (33) considered it to occur "throughout North America, at least east of the Rocky Mountains" where it is "usually abundant [and] frequently cultivated", and that "it has been in cultivation since before the discovery of America . . . [and] its wide distribution is explained by its ancient cultivation." Such statements fail to take into consideration certain ecological principles relating to the complex of factors which have been operative in the present-day distribution of plants. If *H. tuberosus* is an indigenous North American species, it had millions of years in which to migrate in the continuous habitats afforded by the stream systems in unglaciated central and eastern North America, and there is no reason to assume that it was not already established in all the regions, both unglaciated and glaciated, in which it could survive before Indian cultures became aware of its edible tubers. As a floodplain-stream bank species, no more effective agent of propagule dispersal than the nearby streams themselves can be envisioned, and the continuity of all watercourses of the Mississippi drainage, and hence of the *H. tuberosus* habitat throughout this large watershed, presents the probability of a thoroughly-completed geographical distribution of the species long before the advent of man. It seems a better inference that it was widely cultivated by the Indians because it was already widely distributed and readily available, and that their source of plants for cultivation in the Mississippi watershed was nearly everywhere the nearby wild populations.

That sunflower species, not already growing in the soils and climate of Tennessee before the arrival of man, fail to become established in the natural vegetation, although the propagules are abundantly available, is testified to by *H. annuus* and *H. laetiflorus,* both of which are cultivated today in probably every county of the state, but are almost never found far away from their grounds of cultivation. In addition, members of the *"giganteus* group" *(H. giganteus, H. maximiliani, H. grosseserratus)* persist only rarely in the state following apparent introduction.

It is therefore concluded that *H. tuberosus* is as justifiably considered a long-time native Tennessee sunflower as *H. microcephalus* and others, and although plants locally may be escapes from past cultivation, the widespread distribution of the species as a whole in the state is an expression of its past as well as its present ecological adaptation to the soils and climate of most parts of Tennessee.

Helianthus tuberosus is believed to hybridize naturally in Tennessee with *H. hirsutus, H. strumosus,* and perhaps others (see discussions of *H. hirsutus* and *H. decapetalus).* The species is reported to be a hexaploid (14).

(14) *Helianthus giganteus* L. (Fig. 4). Field characters: (1) Leaves alternate, numerous, blades lanceolate and tapering to a short petiole or petiole-like base, obscurely 3-veined; (2) stems rough-pubescent, up to 3 m. tall; (3) disk about 2 cm. broad, rays pale yellow, oval, up to 2 cm. long. Flowering August-September.

This species has been reported but three times in Tennessee: A collection in or near Knoxville, date unknown, by A. Ruth, which was cited by Gattinger (9) in 1901, for which there apparently is no longer a supporting herbarium specimen; a collection from a large and vigorous population on an abandoned, heavily disturbed site in the village of New River, Scott County *(Beatley,* UT 26771, 1959); and a large population on a floodplain in southern Monroe County *(Beatley,* UT 29119, 1961). It is inferred to be a very rarely introduced species in Tennessee. Watson (33) describes it as being "abundant in wet soil throughout the northeastern quarter of the U. S. and adjacent Canada, . . . very common within its range, and [occurring] only sporadically outside it." Doubt of extension of its range very far into southern United States is implied in his statement, "I question its occurrence south of a line drawn from North Carolina to southern Missouri."

The species has been used frequently in experimental hybridization studies of the genus, and naturally-occurring putative hybrids with *H. grosseserratus, H. maximiliani, H. divaricatus,* and *H. mollis* are cited by Long (20) and Jackson and Guard (18). Such crosses are unlikely to occur among *Helianthus* populations in Tennessee because of the rarity of *H. giganteus,* but they are nevertheless possible in areas where *H. giganteus* may become locally established and any of these other species are also growing nearby.

A small population of putative hybrids was observed on a disturbed roadside bank in Monroe County, where the large population of *H. giganteus* referred to above was growing on the floodplain and *H. microcephalus* grew at the borders of the forest on the adjacent slope *(Beatley,* UT 29118, 1961).

The species is diploid (14).

(15) *Helianthus maximiliani* Schrad. (Fig. 4). Field characters: (1) Leaves numerous, at least the upper alternate, blades lanceolate, 1-veined, tapering to a short petiole or petiole-like base, some or all conduplicate and falcate; (3) stems rough-pubescent, around 2 m. high, sometimes colonial; (4) heads in upper part of inflorescence usually short-peduncled (peduncles 1-4 cm. long), very showy, disks 2-3 cm. broad, rays up to 4 cm. long, the margins turned more or less upward and inward ("cupped"). Flowering (in Tennessee collections) from late August to mid-October.

According to Watson (33): "The plant grows readily from seed. . . . The leaves of seedlings are usually opposite below the inflorescence, much larger, less conduplicate, and the internodes longer, and the stem produces abundant branches from even the lower axils. In older plants, however, the stem . . . is always simple unless injured."

This is a western species, uncommonly introduced into Tennessee, although it has been collected to date in 11 counties, especially in the Appalachian Valley in the eastern part of the state. It grows on moist or dry open sites, and is quite distinctive and easily recognized, except when scarcely any of the leaves are conduplicate

and the peduncles are much elongated *(Beatley,* Jefferson Co., UT 26639, 1959).

Naturally-occurring putative hybrids of *H. maximiliani* and *H. grosseserratus* have been reported (21) as have vigorous artificial hybrids between this species and *H. occidentalis* and *H. giganteus* (19). Unless these other species become more widely distributed in the state than it appears they are today, there is little likelihood of their natural hybridization with *H. maximiliani,* except under conditions of cultivation. The species is diploid (14).

(16) *Helianthus grosseserratus* Martens (Fig. 4). Field characters: (1) Leaves numerous, alternate (rarely all opposite), blades lanceolate, obscurely 3-veined, softly pubescent beneath, conspicuously toothed or not, tapering to a short petiole or petiole-like base; (2) stems glabrous, more or less glaucous, up to 4 m. high; (3) disks 1-2 cm. broad, rays up to 4 cm. long, bright yellow. Considered by Watson (33) to be "undoubtedly the handsomest and most graceful of all the sunflowers." Flowering (in Tennessee collections) August-September.

Small (27) specifically mentions Tennessee as being in the range of this species, but no record specimens have been located upon which the inclusion of this state might have been based. It was not cited by Gattinger (9, 10) as a Tennessee species, and the four collections indicated in Fig. 4 are those made in 1957 and 1959, which constitute the only known collections of *H. grosseserratus* from this state. The western ⅓-¼ of Tennessee was included by Long (20) as within its geographical range—an interpolation from its known ranges in Kentucky to the north and Louisiana to the south—but if the species occurs anywhere within this part of the state, as elsewhere in Tennessee, it is apparently as an escape from cultivation or by introduction in some other manner. It is primarily a species of northeastern and north-central United States, but with a southwestern extension of its range into northeastern Texas and eastern Oklahoma.

Putative hybrids of this and a number of other species have been collected elsewhere in the field (18, 19, 20, 21, 22, 24). Of significance to the Tennessee species of *Helianthus* is the evidence from the work of these investigators that rare sunflowers—in Tennessee, *H. grosseserratus, H. giganteus, H. maximiliani, H. occidentalis,* and perhaps *H. salicifolius*—may occasionally hybridize with native species. Where fertile or partially fertile hybrids are produced, local populations of native sunflowers in the state may therefore exhibit the results of introgression from rarely introduced species, the parental stock of which may have long-since disappeared from their past sites of introduction.

(17) *Helianthus laevigatus* T. & G. Field characters: (1) Stem glabrous, somewhat glaucous, solitary, 1-2 m. high; (2) leaves opposite, esssentially smooth and glabrous throughout, blades lanceolate, obscurely 3-veined, serrulate-subentire, tapering to the petiole-like base; (3) disks 1-1.5 cm. broad, yellow, rays up to 2 cm. long, inflorescence few-branched; (4) middle (and perhaps higher) elevations of the mountains of East Tennessee.

This species is included here among the Tennessee species of *Helianthus* largely on the basis of Dr. Gattinger's reference to it in both his 1887 and 1901 floras of the state (9, 10). In 1887, in describing the floristic richness of the cove forests (author's terminology) of the middle elevations of the "subalpine region" of the state, *i.e.,* the mountains, he states that "out of a rich display of herbaceous plants, I would select . . . *Helianthus laevigatus* Torr. & Gray . . .", and although failing to list the species in the floristic list for the state in the same publication, the omission was taken care of in his 1901 "Flora of Tennessee" (10) where its distribution was noted as "Mts. of E. Tenn." His supporting specimens, if any, would have been among those lost with the University of Tennessee herbarium in 1934, and no other specimens apparently are in existence, nor is there mention of the species' occurrence in Tennessee in any edition of the regional floras contemporary with or more recent than Gattinger's work. Although the authors of the regional manuals may have rejected Gattinger's citation of the species in Tennessee because of lack of supporting specimens by either Gattinger or institutional herbaria, the species is sufficiently distinctive, and he apparently was familiar enough with all other members of the genus known to occur in the mountains today, that it is believed the reliability of his citation should be tentatively accepted until the area to which he referred has been more intensively collected for its sunflowers than it has been to date. Moreover, *H. laevigatus* is an endemic of the central and southern Appalachian Mountains, whose range as given in the manuals includes the mountains variously of North Carolina, Virginia, West Virginia, southern Pennsylvania, and in Small (27) Kentucky, and there can be little doubt that the species should be expected to occur in the mountains of East Tennessee as well. It is here included with the anticipation that supporting specimens will be collected in the future.

The ecological status of *H. laevigatus* has been variously interpreted in the literature: Watson (33) states that "the plant grows abundantly on the slopes and summits of mountains"; Britton and Brown (2) considered it a species of "dry soil"; Gattinger, on the basis of the community associates named, placed it in the mesophytic forests of the middle elevations of the mountains, probably in southeastern Tennessee. Core[6] considers it in West Virginia to occur "exclusively in the mountains, at the middle elevations, in dry soil at forest borders."

H. laevigatus is reported to be a tetraploid (14).

(18) *Helianthus eggertii* Small (Fig. 3). Field characters: (1) Stems colonial, smooth and glabrous, purplish and glaucous, 1-2 m. high; (2) leaves opposite, glabrous on both sides, extremely glaucous beneath and less so above, blades lanceolate, obscurely 3-veined, serrulate-subentire, tapering to the petiole-like base;

6 Personal communication, Dr. Earl L. Core, West Virginia University, February, 1960.

(3) involucral bracts lanceolate, acute to acuminate, glabrous except for ciliolate margins, disks 1-1.5 cm. broad, yellow, rays up to 2 cm. long, inflorescence few-branched; (4) "Oak Barrens" of the Highland Rim of Middle Tennessee. Plants are very conspicuous because of the colonial habit and marked glaucescence. They are otherwise distinctive among most of the native sunflowers of the state because of tapering leaf bases and obscurely 3-veined blades. Flowering at peak in early September.

This species is known to date from three counties of the western Highland Rim and from putative hybrids or hybrid derivatives in three counties of the eastern Highland Rim. It was first described by Small in 1903 (26), and the type and isotypes are from a collection by H. Eggert in 1897 from "White Bluff, Dickson County," of which, according to Watson (33) "There are many specimens." Only other Tennessee collections known are the recent ones from Lewis and Lawrence Counties (*Beatley*, UT 22626, 22627, 22632, 1959).[7] The species is probably much more common in the "barrens" country of this region of the state than collections to date would indicate, and should be looked for elsewhere in the western Highland Rim (especially in Hickman County), in the "barrens" of the eastern Highland Rim where putative hybrids or hybrid derivatives have been collected, and on the Coastal Plain Uplands. Watson's referral of it to the "Mountains of Tennessee" is in error (33).

In three additional collections (*Beatley*, UT 26787, 1959, Clay Co.; *Beatley*, UT 25961, 1959, DeKalb Co.; *Beatley*, UT 22587, 1957, Grundy Co.) *H. eggertii* appears to have made genetic contributions to these local populations, either through introgression or direct hybridization with other unidentified parental species (*H. microcephalus* in the case of the DeKalb County population). A chromosome count, indicating that *H. eggertii* is hexaploid (personal communication, D. M. Smith), however, raises problems of the mechanisms of any inferred hybridization of this with diploid species. The status of *H. eggertii* as a parental species of these or any other suspected hybrids, it appears, must await definitive studies of its genetic makeup.

(19) *Helianthus angustifolius* L. (Fig. 4). Field characters: (1) Leaves numerous, usually alternate, distinctly different from those of any other native sunflower—narrowly lanceolate to linear, 10-20 cm. long, up to 1 cm. broad, usually much narrower, 1-veined, revolute, scabrous above, more or less pubescent beneath, tapering to a petiole-like base; (2) stems more or less hispid-pubescent with short hairs, 1-2 m. high; (3) involucral bracts narrowly lanceolate, loose, acuminate; (4) heads and inflorescence branches commonly few, peduncles slender, disk 1-1.5 cm. broad, disk corollas with purple lobes, rays bright yellow, 1-3 cm. long; (5) usually occurring in wet soils, or on sites that are at least seasonally poorly drained. This is the last of the genus to come into flower in Tennessee; flowering begins in early September when all other species are at or past their flowering peaks.

Once its gross aspect is known, this narrow-leaved sunflower is as easily distinguished from other sunflowers and other coarse composites when in the vegetative condition as when in the flowering condition. Watson (33) noted considerable variation in the vegetative characters which he believed to be due to environmental factors, particularly light intensity. Environmental effects upon the expression of these morphological characters, however, could rarely if ever be sufficiently great to result in confusion of this with any other species of vascular plant growing in Tennessee (see discussion of *H. salicifolius*).

Helianthus angustifolius occurs as local and often isolated populations of usually rather numerous individuals, is widespread throughout the state, though on the whole it is a rather uncommon species except locally, and is associated with depressions or other wet to moist sites in regions of strongly acid soils. It is believed to be absent in the calcareous soils of the Central Basin and dissected Highland Rim (except where rarely introduced), and it has not been collected in the mountains outside of Cades Cove in the Great Smoky Mountains National Park. On the Coastal Plain Uplands of the Mississippi Embayment of West Tennessee, especially in the Hardeman-McNairy-Chester County area, locally this is a "weed" species which occurs on a wide variety of sites with respect to apparent soil moisture characteristics, and is not uncommon on what appear to be xeric sites in the southern part of this area.

The species can be expected to occur in the lowlands or topographic depressions in any region where *H. silphioides* or *H. atrorubens* grow, and under some circumstances may be growing on the same site with one or the other of these species. Putative hybrids of *H. angustifolius* and *H. atrorubens* have been reported by Martin (23) to occur elsewhere, and the chances are excellent that they may also occur in Tennessee. The species is diploid (23).

(20) *Helianthus salicifolius* A. Dietr. A species appearing to be closely related to *H. angustifolius*, but distinguished by its (1) glabrous stems, 2-3 m. high, (2) loose and essentially glabrous involucral bracts, and (3) very numerous, closely crowded, drooping, narrow (1-3 mm. wide) leaves, giving the plant an elongated plume-like or "bushy" appearance. Flowering August-October (11).

Helianthus salicifolius occurs as a native species on calcareous soils (32) in northeastern Texas, eastern Kansas and Nebraska, and western Missouri and Arkansas (20), but is found outside this range as a cultivated species or escape from cultivation. Although it has not been looked for in cultivation in Tennessee during the present study and there are no known herbarium specimens of "escapes", it doubtless is planted as an ornamental in the state, and is therefore included here. It could be expected to be at least as frequently

7 Additional Tennessee collections have been made by Dr. Dale M. Smith, who states (in personal communication) that he has collected the species also in Kentucky and refers his specimens to **H. strumosus.** Since it is so very distinct from any other species of **Helianthus** observed throughout the State of Tennessee in the course of the field work of the present study, and unlike any of those to which the epithet **H. strumosus** has been attached in the University of Tennessee collection of the genus, its recognition as a species is here retained.

planted in Tennessee as in the northeastern and north-central states, where Long (20) reports it to be "occasionally cultivated" and its occurrence to be "attributable to garden varieties or escapes", because of the geographic proximity of Tennessee to the region in which it is indigenous and similarity of the human cultures in some areas. It could also be expected to become established out of cultivation perhaps more readily in Tennessee (in areas where its edaphic requirements may be met) because of the closer affinities of the state's macroclimate to that of the region in which it is native.

Doubtful Species

Helianthus verticillatus Small. In 1898 Small (25) described a new species of *Helianthus* from specimens collected a few years previously in Chester County:

> The prolific flora of Tennessee makes it necessary to add another member to the genus Helianthus. The specimens in question were collected by Prof. S. M. Bain at Henderson, Tennessee, in August, 1892, no. 288. *Helianthus verticillatus* is related to *Helianthus giganteus,* but is easily distinguished by the smooth and glabrous stems, the narrower entire smoother leaf-blades and the narrowly linear-lanceolate bracts of the involucres.

Bain's collections (two specimens NY, one specimen US) so far as is known are the only ones ever made of this species, and the original description and all references to its taxonomic characters since that time have been based upon the type collection. It is not known whether or not the type collection may have consisted of stems from a single colony.

The plants are characterized by the following: Perennial, stems 1-2 m. high, smooth and glabrous, becoming scabrous in the inflorescence branches; leaves in whorls of 4, reduced ones in inflorescence mostly opposite, blades linear-lanceolate, 1-veined, 8-10 cm. long, 1-1.4 cm. broad, acuminate, entire, somewhat revolute, short-scabrous or shagreen-like above, finely pubescent beneath, tapering into short petioles or petiole-like bases; inflorescence few-branched, branches closely ascending, heads several; involucral bracts about 1 cm. long, narrowly linear-lanceolate, ciliolate, otherwise nearly glabrous, loose and somewhat spreading; rays yellow, about 2 cm. long; disks about 1 cm. broad, disk corollas yellow. Described by Bain as occurring on "low grounds", and by Small (25) "in wet sandy soil."

Watson (33) considered this "a very distinct plant." Although no special significance would be attached to whorled leaves in themselves, since three leaves at a node may occur not infrequently in individuals of several species of the genus, the condition of four at a node is exceptional in the species of *Helianthus;* and the plants are so distinct from any other species of *Helianthus* in Tennessee (or elsewhere) that they cannot be dismissed as merely a local variation of some other species.

That the specimens belong to the *"giganteus* group" is evident from the narrowly lanceolate, 1-veined leaves, which taper gradually to the base, and this is especially noteworthy because of the scarcity of species of this group in Tennessee (the one representative of the group which is native being *H. angustifolius).* Morphologically the leaves should probably be considered opposite, although the doubling of number of leaves at each node might be related to an unusual phyllotaxy resulting from expression of opposite and alternate arrangements simultaneously. Smoothness of the stem and upper surface of the leaves, presence of more than one leaf at a node and relatively long internodes, over-all leaf length/width ratio, subglabrous ciliate involucral bracts, and yellow disk corollas, are characters in combination which suggest relationship to *H. eggertii;* and the short pubescence of the leaves beneath, the 1-veined character and relative narrowness of the leaves in relation to width, their somewhat revolute margins, and the occurrence of the plants in "wet" soils, are highly suggestive of *H. angustifolius,* which is perhaps the commonest sunflower of the southern Coastal Plain Uplands in which Chester County is located.

The closest known station for *H. eggertii* is about 70 mi. ENE (Lewis County, 15 mi. ESE of Hohenwald), but the distribution of *H. eggertii* is very imperfectly known to date and its occurrence in the southern part of the Coastal Plain Upland as well as in the "Oak Barrens" of the southwestern Highland Rim can be anticipated since the soils and vegetation of the two regions are similar in many respects. There is suggestion of hybridization of *H. eggertii* with other species on the eastern Highland Rim, 100 or more miles from the nearest presently known station of *H. eggertii* (see discussion of *H. eggertii). H. verticillatus* does not resemble any of the other native sunflowers of the State, and there appears to be no need for postulating a rarely introduced member of the *"giganteus* group" as one of the parental species.

The plants (or plant) described by Small are, therefore, here tentatively considered to be of hybrid origin, with *H. angustifolius* and *H. eggertii* the most likely parental species. Until specimens of *H. verticillatus* can be found again in the field, and studies made which demonstrate it to be a definable and self-perpetuating population, the status of this as a valid species must remain in doubt.

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THE EIGHTEENTH TENNESSEE SCIENCE TALENT SEARCH

(Continued from Page 134)

program which develops a scientific attitude and a drive for research long before the high school senior year. Tennessee is fortunate to have such a program in its Junior Academy of Science, which is open to all students from grades 7 through 12.

In 1963 the Junior Academy was active throughout the 11 regions of the state. The Regional Science Day Conferences were attended by over 230 students. Winners in the regional competition participated in the State Science Day competition held in March at George Peabody College. Eight state winners were selected in four science fields. From these a Grand Prize winner was selected to represent the Tennessee Junior Academy of Science at the December meeting of the American Association for the Advancement of Science to be held in Cleveland, Ohio. Brian J. Delano from Tullahoma High School won this honor and will present a paper on his project, "Space Vehicle Attitude Control."

The National Science Seminars, sponsored by the New Mexico Academy of Science, in Albuquerque, were attended by approximately 200 students from Tennessee. Dr. John Hopperton, Director of the National Science Fair-International, had organized the seminars, which were conducted by a number of eminent scientists.

The final program of the school year, sponsored by the Tennessee Academy of Science, Union Carbide Nuclear Company, and the Oak Ridge Institute of Nuclear Studies, was held at Oak Ridge to honor all winners in the Tennessee Science Talent Search and the State Science Day Competitions. A special tour of the Oak Ridge National Laboratory facilities was arranged by Dr. Chris Keim, Director of Technical Information, ORNL. Following the Honors Banquet, Dr. Alvin M. Weinberg, Director of ORNL, spoke to the group on the making of potable water for peoples of all the world.

1963 Talented Science Students

Below is the list of talented science students, listed by cities. In each case the student's name and the title of his science project are listed first, then the teacher's name and the school. An asterisk (*) indicates that the student received recognition also in the National Science Talent Search competition; (TJAS) indicates the student was a winner in the State Science Day competition; all other students were winners in the State Science Talent Search.

Bell Buckle

William E. Gallagher, The Relationship Between Metabolism, Ingestion and Thyroxin; K. G. Tidwell, The Webb School.

Bristol

Fletcher R. Bingham, Comparative Feeding Behavior of Warblers; R. K. Burk, Tennessee High.

Centerville

David B. Beale, Relationships Between Roots and Powers; Hayes Blackwell, Hickman County High.

Chattanooga

Thomas H. Gladney, The Auto-Draftsman; Sister Hyacinth, Notre Dame High.

GEORGE E. HARRISON, III, Coordinate Bond in the Copper (II) Ion; P. D. Greer, McCallie.
VICTOR C. PANGLE, Quantitative Analysis of Boiler Water to Determine Iron Content; Sister Hyacinth, Norte Dame High.

Clarksville
WILLIAD D. EVANS, JR., Fuel Cells; Kenneth Stier, Clarksville High.
LAURIE H. LYLE, Effect of Radiation on Chicken Embryos; Mrs. Ruth Rice, Clarksville High.

Cleveland
DONALD B. BATCHELOR, A Magnetohydrodynamic Plasma Jet; L. M. Kresse, Bradley Central High.

Dyersburg
JOHN J. REED, Effects of Polarization on Antenna Gain; C. B. Camp, Jr., Dyersburg High.

Holladay
KAREN A. HENDRIX, Intravenous Saline Effects—An Osmotic Function; Mrs. Lydia Branch, Holladay High.

Kingsport
PHIPPS ARABIE, Spectroscopy; Charles Wise, Johnson City High (TJAS).
JUDY PAULEY, Staining Blood Cells; Charles Wise, Robinson Jr. High (TJAS).
LAWRENCE H. REID, The Irradiation of Cattle Sperm; J. T. Davis, Dobyns-Bennett High.
WILLIAM A. RESCH, III, The Optical Maser; J. T. Davis, Dobyns-Bennett High.

Knoxville
ERNEST CHILDS, Chromatographic Studies on Plants; Lula Mae Shipe, Central High (TJAS).

Memphis
*ROBERT S. CARNEY, JR., Nerve and Muscle Tissue Responses to Alternating Current; Frances B. Wild, White Station High.
MICHAEL B. CASINI, Use of Turtle Red Blood Cells in Hemagglutination Test; Bro. Lawrence Justin, Christian Brothers High.
*PHILLIP T. EMERICK, Measurement of Lunar Formations; J. D. Reding, Treadwell High.
CHARLES S. FOSTER, The Magnetic Susceptibility Balance; Bro. Lawrence Justin, Christian Brothers High.
ALFRED G. KASSELBERG, Construction and Characteristics of Silicon Solar Cells; B. G. Young, East High.
*CHARLES H. KITCHENS, Petrology and Structural Aspects of Precambrian Sills in the Pony Gneiss of South London Hills, Madison County, Montana; R. E. Jonakin, Messick High School.
SHIRLEY L. NEWTON, Is Irradiation of Seeds Beneficial to Plant Growth? J. D. Reding, Treadwell High.
FRANK C. WHISMAN, Two-Phase Materials; Joe F. Summers, Oakhaven High.
JACQUES F. YATES, Matter and Forces in Fluids; Sister Mary Kilian, Father Bertrand High.

Murfreesboro
WALKER F. TODD, The Effects of Weather in Murfreesboro for the Years 1960-1963; Mrs. Mary Miller, Murfreesboro Central High.

Nashville
JANET FLAGG, Polio Virus and Tobacco Mosaic Virus; Leslie L. Cranes, Washington Junior High (TJAS).
JOHN E. KOLEMBA, Theory of Formation of an Un-isolated Chemical Bonding Structure; Mrs. Burt Francis, Isaac Litton High (TJAS).
DANNY M. NEWMAN, A Digital Computer for Class Demonstration; Mrs. Burt R. Francis, Isaac Litton High.
JAMES C. SEAY, Diffusion Cloud Chamber; Jacquelyn Turner, Hillsboro High.
WILLIAM P. WEATHERLY, Calorimetry; Jacquelyn Turner, Hillsboro High (TJAS).

Oak Ridge
JAMES C. BARTON, Chemical Abscission and Phytochrome Stimulation in Wheat; Mrs. Angie Perry, Oak Ridge High.
*DAVID ALAN CULVER, Effects of Infra-red and Ultra-violet Light on Germination and Growth of Lettuce Plants; Mrs. Angie Perry, Oak Ridge High.
RUSSELL M. NORTON, The Effect of Subzero Temperatures on Yeast; S. D. Sheppard, Oak Ridge High.
LAWRENCE P. RIORDAN, Oxide Films on Niobium; S. D. Sheppard, Oak Ridge High.
*SERENA SAVAGE, Color and Eye Adaptation; Mrs. Angie Perry, Oak Ridge High.
*BENJAMIN H. TEAGUE, III, Non-Standard Matrix Operations; S. D. Sheppard, Oak Ridge High.

Pikeville
GREGORY ANDERSON, Measuring a Molecule; Carl Boynton, Mountain Crest High (TJAS).
WILLENE MCREYNOLDS, Metabolism and Life Processes; Mrs. Thelma Boynton, Bledsoe County High (TJAS)

Smyrna
JAMES M. CRYER, Vulnerability of Glass to Attack by Alkalis; Mrs. Clyde Richards, Smyrna High.
ROGER ALAN SHIER, Electroplating of Copper; Mrs. Clyde Richards, Smyrna High.

Tullahoma
BRIAN J. DELANO, Space Vehicle Attitude Control; James Kemp, Tullahoma High (TJAS).
EVERETT E. MUNN, A Particle Accelerator; James Kemp, Tullahoma High.

NEWS OF TENNESSEE SCIENCE

(Continued from Page 125)

The 1964 schedule of training courses in the diagnostic application of radioactive isotopes has been announced by ORINS. The courses, administered for the AEC, are designed to provide minimal basic training and clinical experience in the safe handling of radioactive materials to qualify physicians for AEC licensure to use radio-isotopes on patients. Information about the courses, fees, dates and application forms may be obtained from Dr. Ralph T. Overman, Special Training Division, ORINS, P. O. Box 117, Oak Ridge.

A computer center is now in operation at East Tennessee State University, under the direction of Stanford Johnson, Associate Professor of Mathematics.

A separate Department of Engineering Mechanics has been established in the University of Tennessee College of Engineering and is conducting courses heretofore given under the administration of the Civil Engineering Department. The new Department is headed by Dr. Fred N. Peebles, Professor of Chemical Engineering at UT.

Clarence C. Lushbaugh, M. D., pathologist recently with the Los Alamos Scientific Labratory, of the University of California, has joined the ORINS Medical Division staff. At Oak Ridge he will extend his research in radiobiology, particular as it applies to man, and the diagnosis and treatment of certain diseases through the use of isotopes.