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A REVISION OF THE GOLDENASTER GENUS *CHRYSOPSIS* (NUTT.) ELL. NOM. CONS. (COMPOSITAE-ASTEREAE)

JOHN C. SEMPLE

The genus *Chrysopsis* (Nutt.) Ell. is a yellow rayed member of the Tribe Astereae of the Family Compositae with $x = 5$. It has never before been monographed with the limits recognized here. Excluded from the genus are all the grass-leaf goldenasters (*Pityopsis* Nutt.), the prairie goldenasters (*Heterotheca* Cass. sect. *Phyllotheca* (Nutt.) Harms), and the two species of sect. *Ammodia* (Nutt.) Harms of *Heterotheca*, all of which have been included in *Chrysopsis* by some authors. A list of all the taxa of the three goldenaster genera was given in Semple, Blok, and Heiman (1980). The affinities of the genus are with the lower chromosomal base number genera of the tribe. It is most closely related to *Bradburia*, less so to *Xanthisma* and *Croptilon*, and more distantly to *Macheranthera* sensu lato. This group of genera with $x = 5$ or $x = 4$ includes annuals, monocarpic perennials (usually biennials), and short-lived perennials. All have dentate-serrate to pinnatifid basal rosette leaves. All have one acrocentric satellite chromosome with the nucleolar organizer region that divides the short arm into subequal portions. In this group are included species with a double pappus whorl crowning the fruit and species with only one pappus whorl on the fruit. Most are endemic to the southeastern United States in the broad sense.

Chrysopsis as treated here consists of 10 species native to the southeastern United States, particularly Florida (Fig. 1). Only three derived species occur elsewhere in the United States; *C. pilosa* on the Ozark Plateau and surrounding areas; *C. mariana* on Long Island, N.Y., southward to Florida and westward to Ohio and

Texas; and members of the *C. gossypina* complex on the coastal plain from Virginia to Louisiana.

HISTORICAL REVIEW OF THE GENERIC NAME AND LIMITS

The name *Chrysopsis* first appeared in the literature in 1818 in T. Nuttall's *The Genera of North American Plants* as a sectional name under the genus *Inula* L. Elliott (1824) subsequently raised the name to generic status, *Chrysopsis* (Nutt.) Ell., which has been conserved over the earlier name *Diplogon* Raf. a *nomen rejeciendum* (International Code of Botanical Nomenclature, 1972). In more recent times the generic status was questioned by Shinnars (1951), who merged *Chrysopsis* into *Heterotheca* Cass. Most recently Semple (1977) proposed that part of Elliott's genus be recognized at the generic level and part be transferred to *Heterotheca*. Thus considerable confusion has developed over the proper generic name to place in front of the type species of the *Chrysopsis* group of taxa. Linnaeus (1753) described the type species as *Inula mariana* L. The combination *Chrysopsis mariana* (L.) Ell. was proposed in 1824. The combination *Heterotheca mariana* (L.) Shinnars was made in 1951. Elliott's combination is considered proper and is used in this revision.

The concept of the genus or section *Chrysopsis* has varied greatly during the past century and a half. Nuttall (1818) included in his *Inula* sect. *Chrysopsis* the species native to North America having double pappus and naked anther bases. In this assemblage were: 1) species of *Chrysopsis* as defined here; 2) species of the grass-leaf goldenaster genus *Pityopsis* Nutt., e.g., *P. graminifolia* (Michx.) Nutt.; 3) species of *Heterotheca* sect. *Phyllothea* (Nutt.) Harms, e.g. *H. villosa* (Pursh) Shinnars; 4) a member of *Heterotheca* sect. *Heterotheca*, *H. subaxillaris* (Lam.) Britton & Rusby (listed as *Inula scabra* Pursh); and 5) several species of *Aster* without yellow ray florets, e.g., *A. linariifolius* L.

Elliott (1824) removed the species of Astereae from Nuttall's *Inula* of the Inuleae. He emphasized the yellow ray floret color in his genus *Chrysopsis* by excluding *A. linariifolius*, by retaining the heterocarpic *H. subaxillaris* as *Chrysopsis scabra* (Pursh) Ell., and by including *Croptilon divaricatum* (Nutt.) Raf as *Chrysopsis divaricata* (Nutt.) Ell. This last species is frequently treated as *Haplopappus* (sect. *Isopappus*) *divaricatus* (Nutt.) Gray. Otherwise Elliott included in *Chrysopsis* all that Nuttall had.

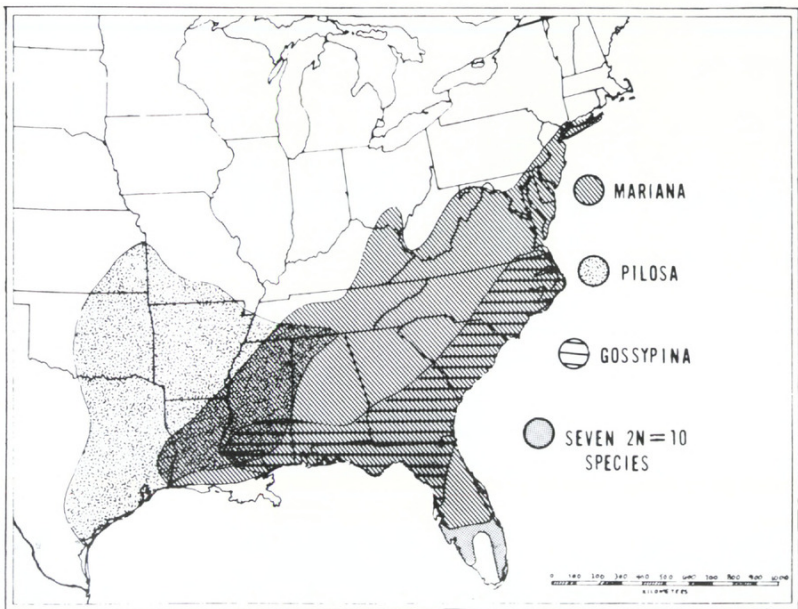


Figure 1. The distribution of species groups in *Chrysopsis*. Superimposed on a state outline map of the eastern United States are the ranges of the four groups of taxa. *Chrysopsis mariana* and *C. pilosa* are $x = 4$ taxa and have specialized morphologies. The *gossypina* complex is of allopolyploid origin and has $x = 9$. All the $x = 5$ diploid species are endemic to Florida.

Most botanists have accepted Elliott's concept of *Chrysopsis* with only a few alterations (Fig. 2). DeCandolle (1836) described several new taxa that properly belong in *Heterotheca* sect. *Phyllotheca*, but were included in *Chrysopsis*. Torrey and Gray (1842) described additional new taxa belonging to sect. *Phyllotheca* as well. Nuttall (1841) treated the grass-leaf taxa as a separate genus *Pityopsis*, thus reducing the limits of *Chrysopsis*. The number of species described and placed in *Chrysopsis*, but belonging in either *Heterotheca* or *Pityopsis* steadily increased through the latter half of the eighteen hundreds. By the turn of the century the number of species generally included in *Chrysopsis* was sufficiently large that it had become difficult for any one person to carefully examine all the species in detail.

The treatments of Bentham and Hooker (1876) and Gray (1884) have been followed by many tradition-minded botanists of the twentieth century, e.g. Cronquist (1977, 1980). A broadly delimited genus *Chrysopsis* was accepted by Keck (1960), Steyermark (1963), Barkley (1968), Seymour (1969), and Boivin (1972) in their floristic

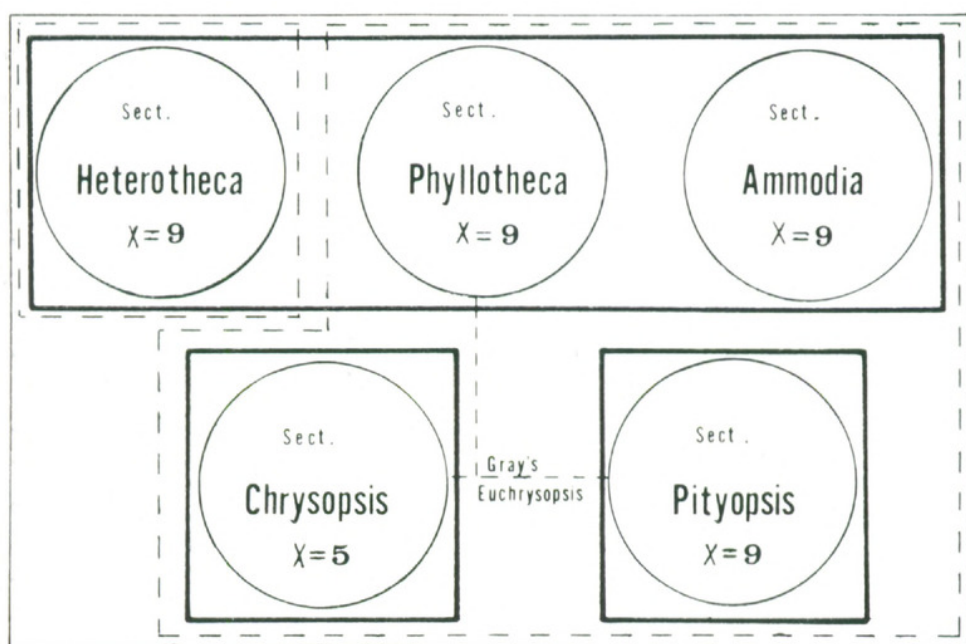


Figure 2. Generic placement of the five sections of goldenasters. Three genera were recognized by Semple, Blok, and Heiman (1980)—thick lines. Elliott (1824) and Gray (1884) and others recognized a large genus *Chrysopsis* and a small genus *Heterotheca*—broken thin lines. Gray included both sect. *Pityopsis* and sect. *Ammodia* in his large sect. *Euchrysopsis*. Shinnery (1951), Harms (1974) and others placed all sections into one genus *Heterotheca*—thin line.

treatments of different regions of North America. Small had recognized *Pityopsis* at the generic level in 1903, but in 1933 he merged it with *Chrysopsis*, abandoning Nuttall for Gray.

Other twentieth century botanists have taken a different view of the status and limits of *Chrysopsis*. When Shinnery (1951) merged *Chrysopsis* into *Heterotheca* he did so on morphological grounds. He noted that the lack of a pappus on the ray floret fruits of *Heterotheca* was not absolute in separating the two genera. Some individuals of the usually heterocarpic *H. chrysopsides* DC. occasionally produced ray floret fruit with a bristly pappus. The merger was substantiated on cytological evidence, or so it appeared, by Harms (1965). Shinner's concept of a single goldenaster genus *Heterotheca* was adopted in regional floras by Radford et al. (1968), Correll and Johnston (1970), and Long and Lakela (1971). Bowers (1972) treated *Pityopsis* as a section of *Heterotheca* in his revision of the grass-leaf goldenasters. Harms (1974) treated *Chrysopsis* along with *Pityopsis*, *Ammodia*, and *Phyllothea* as sections of *Heterotheca* and included in his conspectus of the section *Chrysopsis* a key to the sections of the genus.

The concept of *Chrysopsis* followed in this revision was first presented in a paper on the cytotaxonomy of the goldenasters (Semple, 1977). Harms (1965) had based his support for *Heterotheca* sensu Shinnery on an experimental hybrid between *H. latifolia* Buckley and what he referred to as *Chrysopsis berlandieri* Green, a member of the *villosa* complex of sect. *Phyllothea*. Both taxa had $2n = 9_{II}$, as did the hybrid. Semple, Blok, and Heiman (1980) have noted the morphological similarities between the two parental species and the differences between these two and members of the genus *Chrysopsis* as delimited in this revision. They suggested that a "better" name for the "Chrysopsis" species Harms worked with is *Heterotheca canescens* (DC.) Shinnery.

The fact that no intergeneric hybrid had been made other than nomenclaturally was noted previously by me (Semple, 1977) along with observations on karyotype differences between members of *Heterotheca* and members of *Chrysopsis*. Species of *Heterotheca* and *Pityopsis* have a base number of $x = 9$, chromosomes ranging from one to three nanometers (nm), while species of *Chrysopsis* have a base number of $x = 5$ or derived base numbers of $x = 4$ and $x = 9$. The chromosomes range in size from approximately two to seven nanometers. Semple and Chinnappa (1980a & b) have

documented the allopolyploid origin of the $n = 9$ taxa in *Chrysopsis* and described in detail the karyotypes of all the species of the genus.

The similarity between flavonoid profiles of all the species of *Chrysopsis* was noted casually in Semple (1977). The patterns of ray floret, disc floret, and leaf extracts were examined in all species and compared with patterns obtained from extracts of similar tissues from species of *Heterotheca* and *Pityopsis*, which differed significantly from those of *Chrysopsis*.

There is no reason other than conservatism for treating *Chrysopsis* in any way but that done here. The cytological and morphological links thought to have existed between the groups of goldenasters do not exist. Whether or not *Pityopsis* and *Heterotheca* are congeneric is beyond the scope of this revision. The merger of *Pityopsis* into *Heterotheca*, however, was the result of *Pityopsis* being considered a part of *Chrysopsis* sensu lato. Thus the long history of the recognition of the goldenasters as a group of genera has been replete with assumptions about relationships which later have been shown to be only the products of nomenclature or overactive imaginations. Desire to maintain one or two large genera apparently has been the primary cause for such misconceptions.

TAXONOMIC UNITS, THE VALUE OF CYTOLOGICAL DATA, AND THE TRICHOPHYLLA PROBLEM

One man's section may be another man's genus, and there is no criterion or set of criteria that can definitively determine who is right.

A. Cronquist (1977), p. 218

The above statement is generally true about all similar taxonomic levels and particularly so about infraspecific taxonomic ranks. This is frequently also true when no new data have been gathered by one botanist revising another botanist's treatment of a group. In the case of *Chrysopsis* a great deal of new evidence has come to light very recently (Semple, 1977, 1978a and b; Semple, Blok, & Heiman, 1980; Semple & Chinnapa, 1980a & b). The new evidence indicates that the decision to treat *Chrysopsis* as a genus or a section of *Heterotheca* does not fall within the bounds of what Dr. Cronquist has noted as a major difficulty in taxonomy.

The number of genera that one divides the goldenasters into and the number of species that one recognizes within *Chrysopsis* here

depends greatly upon the significance given to cytological data by the individual doing the splitting or lumping. How much cytological variability one is willing to tolerate within a taxon becomes critical, when cytological data are considered very important. A danger in being dogmatic arises because there are so many kinds of cytological variation which are not always carefully distinguished. The amount of variability in a taxon like *Claytonia virginica* L. (Lewis & Semple, 1977), which has 54 known cytotypes based on $x = 6, 7$, and 8 , cannot be equated with the variation in chromosome numbers reported for species with B-type accessory chromosomes, e.g. *Xanthisma texanum* DC. (Semple, 1976), or with the variation in chromosome numbers reported for some genera, e.g. *Crepis* (Babcock, 1947). In short, even though considerable cytological variation is generally accepted to occur within one taxon, it is counter-productive to assume that considerable cytological variability is acceptable in every taxon. The nature of the variation and the nature of the taxon it occurs in must be evaluated in each situation.

In the tribe Astereae a wide range of cytological situations exists at the generic level. For example, the Australian genus *Brachycome* Cass. includes a full documented, aneuploid series from $n = 9$ to $n = 2$ all within a single morphological complex (Grau, 1977). The North American genus *Astranthium* Nutt. includes plants with $2n = 6, 8, 10, 12, 16, 20, 24$, and 36 . The primary base number of the genus is $x = 5$, with $2n = 8$ and 16 based on $x = 4$, and $2n = 6, 12, 24$, and 36 being based on $x = 3$ (DeJong, 1965). From the sporophytic numbers alone base numbers of $x = 6$ and $x = 8$ might also be postulated to expand the range of the base numbers arbitrarily. This interpretation of the chromosome count data would make the genus appear to be cytologically parallel to *Brachycome*, both having long aneuploid series. But, in using cytological data in systematic studies, it is not enough to know reported numbers. Knowledge of the ploidy level and karyotype morphologies is critical for meaningful interpretation. Such data have shown that there are no base numbers of $x = 6$ and $x = 8$ in *Astranthium* and thus it is not cytologically parallel to *Brachycome* at all.

In the case of *Chrysopsis*, Harms (1974) assumed the existence of an aneuploid series with $x = 9$ as primitive and $x = 8, 7, 6, 5$, and 4 as derived. Counts of $n = 4, 5, 9$ and 12 were known at the time. The $2n = 12_{II}$ count for *C. mariana* was assumed to be based on $x = 6$, the mitotic karyotype not having been studied. Only a third of the taxa

had been counted in fact. By not making assumptions about the existence of certain base numbers necessary for a particular taxonomic interpretation, but rather by actually determining chromosome numbers from both meiosis and mitosis, the actual situation in *Chrysopsis* has been discovered (Semple, 1977; Semple and Chinnappa, 1980a and b). No evidence of a long aneuploid series has been found, and in fact $x = 5$, not $x = 9$ is basic for the genus. The presumed $x = 6$ species *C. mariana* has $x = 4$, and the $x = 9$ taxa are allopolyploid hybrids between the $x = 5$ and $x = 4$ phylogenetic lines. In the absence of any cytological links *Chrysopsis* has to stand apart from the other goldenaster genera, unless many ad hoc assumptions about extinct intermediates are made. Such assumptions are easier to accept if cytological data are not viewed as critical. I find it unacceptable to have sections with radically different cytological characteristics placed in the same genus which is defined by only one or two shared morphological characteristics. Thus, the low base number group of goldenasters was recognized at the generic level and not as a section of an otherwise high base genus. Such botanists as Arthur Cronquist (pers. comm.) do not find it unacceptable to have sections with significantly different cytological characteristics in the same genus and therefore have grouped high base number sections with the low base number section into a single large genus *Chrysopsis*.

Within *Chrysopsis* as defined here no sections are recognized nomenclaturally, although several species complexes can be recognized on cytological grounds. The reticulate nature of evolution in the genus makes it impractical to name these groups formally (Fig. 3). If no allopolyploidy had occurred, thereby recombining characteristics of the separate diploid lines, then the genus would be practicably divisible into sections. However, the allopolyploid *gossypina* complex does exist and so it is only useful to discuss the groups informally. This is done in detail in the section on relationships within the genus.

A comparison between my treatment of *Lasallea* Greene amend. Semple and Brouillet, and my treatment of *Chrysopsis* is useful here. Both genera are small, each with fewer than a dozen species by and large native to the southeastern United States, and both have a base number of $x = 5$. In *Lasallea* there were no allopolyploids to blur the lines of evolution (Semple & Brouillet, 1980). Also the differences between species groups were more pronounced than in

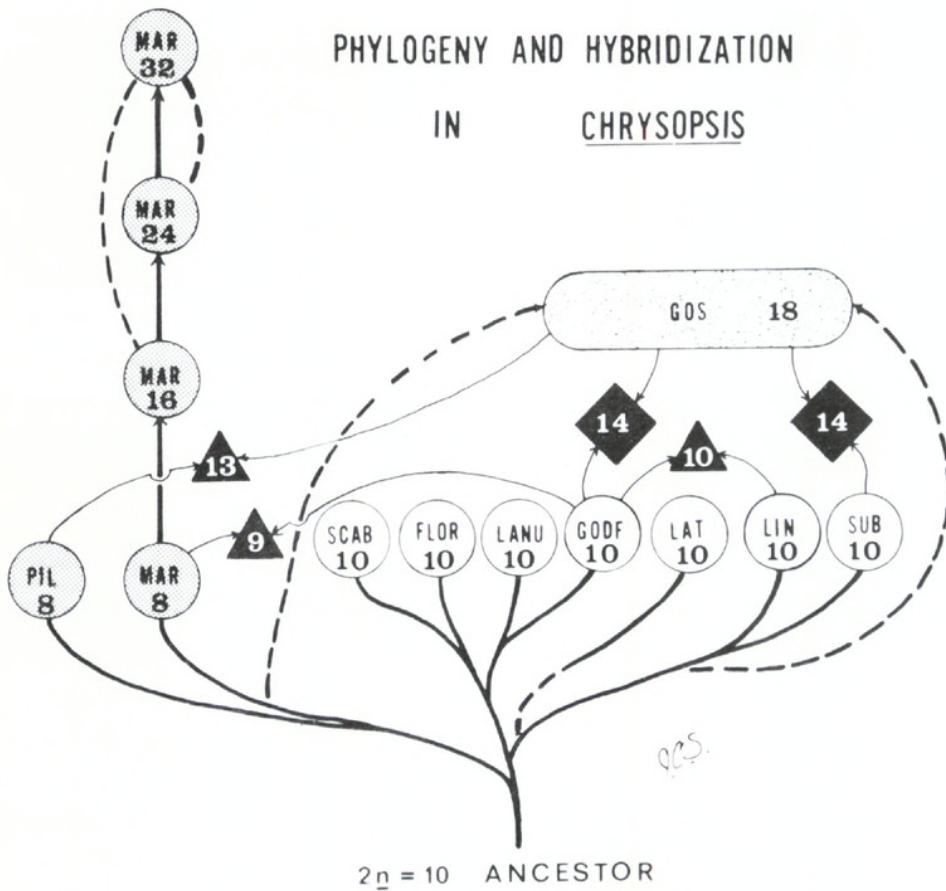


Figure 3. A hypothetical phylogeny of the genus *Chrysopsis*. The nine diploid species (circles) are thought to have evolved from a common ancestor as indicated by thick lines. The $x = 4$ line (shaded circles) includes one polyploid series with alternative derivations of higher ploidy levels indicated by broken lines. The allopolyploid *gossypina* complex (stippled) is thought to have arisen by hybridization between the two diploid lines indicated by thick broken lines. The number in each enclosure is the sporophytic number of the taxon or hybrid. Solid diamonds indicate interspecific hybrids found in nature. Solid triangles indicate experimentally produced interspecific hybrids. Parental species are joined to the hybrids by thin lines.

Chrysopsis, although again not so much so as to bar hybridization between morphologically very distinct taxa. In *Lasallea* sections were recognized, the names already having been proposed under *Aster* for the most part. In *Chrysopsis* no names have been previously proposed that can be usefully applied here. The names proposed by Small (1903) would only confuse matters more. There is little to be gained by proposing additional names.

The criteria used to delimit species vary from one taxonomist to another and from one group to another. This is certainly the

situation in *Chrysopsis*. For example, Small (1903, 1933) recognized 13 species, while Harms (1974) recognized only seven. Ten species are recognized here. In each treatment the species have rather different limits and can only be compared with difficulty in some cases. Knowledge of chromosome numbers and interpretation of these data have made the treatment given below the most unusual. The somewhat unorthodox approach of beginning *de novo* was employed. Cronquist (1977) criticized L.H. Shinnars for this method in connection with the goldenasters. The various keys available and the differences in species interpretation, however, made it necessary to start at the beginning with the plants themselves rather than with the literature.

The state of confusion generated by the contrasting opinions on the status of the taxa *Chrysopsis trichophylla*, *C. subulata*, and *C. lanuginosa* was particularly deep. Dress (1953), for example, completely ignored the last taxon, while Harms (1974) placed it into synonymy under *C. gossypina*. In another instance, the relationship between *C. floridana* and *C. mariana* postulated by Fernald (1937) and restated by Harms (1974) was very misleading, since undue emphasis was placed on the perennial habit of the two species. The actual form of the perennality, the degree of pubescence, and the kind of hairs were not recognized as critical. In short, the level of understanding was such that more than "tidying up" an earlier published revision was necessary.

Species were defined on sets of characteristics with chromosome number, glandularity, phyllary shape, and capitulescence type receiving the greatest weighting. All the diploid species (both $x = 5$ and $x = 4$) are well defined on morphological grounds alone; variation between these is generally discontinuous. The allopolyploid complex, however, is extremely varied morphologically and is only well defined by its $2n = 18$ chromosome number. The "pillar complex" nature of a portion of the genus is represented diagrammatically in Fig. 3. Each "pillar" is well defined and given species status. The overtopping "roof" group is treated as a single species as well, since the morphotypes intergrade fully and can not even be distinguished cytologically. An alternative approach would have been to lump under a few names the following groups of species and have a few very broadly defined species: *Chrysopsis scabrella* ($n = 5$), including *C. floridana*, *C. godfreyi*, and *C. lanuginosa*; *C. mariana* ($n = 4, 8, 12, 16$); *C. pilosa* ($n = 4$); and *C. gossypina* ($n = 5$

& 9) including *C. linearifolia*, *C. hyssopifolia*, *C. subulata*, *C. trichophylla*, and *C. decumbens* with *godfreyi* and *decumbens* linking the first and last assemblages. In the past, authors have tended to separate one or two of the listed species on the basis of a single characteristic that often had no real value, e.g., Small (1903) used phyllary shape. While not a useful key character, chromosome number does have absolute value in separating the *gossypina* complex from the other species of the genus. Furthermore, any suspected hybrids between this complex and any other species would be easily identifiable as such by chromosome number alone.

Subspecies were recognized in two species. Both cases fall within the philosophical bounds of the problem referred to in the opening quote of this section of the paper. I followed the definition of subspecies given in my treatment of *Xanthisma* (Semple, 1974), in which distinct morphology and nearly allopatric distributions were emphasized. The subspecies of *C. linearifolia* were recently described (Semple, 1978b). In this case the morphological differences involved both leaf shape and the kind of capitulescence. The occurrence of a few individuals of the Florida peninsula morphotype, subsp. *dressii*, within the panhandle Florida distribution of the type subspecies made it unsound to recognize each morphotype at the species level, though someone else might wish to do so.

Included in *Chrysopsis gossypina* are three semi-allopatric subspecies. These integrate in the respective zones of sympatry to such an extent that treating each as a species also would have to be done on an arbitrary basis. When only the investiture of the involucre is artificially considered to be of three kinds, then the *gossypina* complex can be split into three groups. Plants with densely woolly heads are similar to Michaux's type collection of the species and Fernald's type collection of *C. longii*. Plants with glabrous or glabrate heads are similar to the type collections of *C. trichophylla*, *C. hyssopifolia*, *C. gigantea*, *C. cruiseana*, and *C. mixta*. This last group was treated as *C. trichophylla* by Harms (1974) who included the distinct $x = 5$ diploid species *C. subulata* as well.

Members of the glabrous-headed subset of the *gossypina* complex, however, are heterogeneous for such traits as habit, degree of leaf pubescence, leaf shape, kind of capitulescence, involucre size, and the nature of the upper stem and peduncle indument. When these traits are considered along with head investiture (which really

does not occur in three distinct kinds) then the glabrous-headed subset is seen to merge into the other two subsets to such an extent that it is not possible to subdivide the complex in this traditional manner.

The *gossypina* complex can be divided into subunits when sets of characteristics are compared. Two subunits can be separated out on the basis of morphology and distribution, and these have been given subspecies status. Subspecies *cruiseana* inhabits the Gulf coast barrier islands of western Florida and Alabama. Over much of the subspecies' range populations contain only individuals with the following characteristics: stems decumbent or spreading from a perennial base, stem leaves small and glabrous, stems glabrous and often red-tinted, capulescence subumbellate-cymose with a few heads, phyllaries glabrous and generally appressed. In populations that occur on parts of the barrier island system which are in contact with the mainland, individuals with a combination of these traits and those of subsp. *hyssopifolia* have been collected. Hybrids between subsp. *cruiseana* and subsp. *gossypina* also have been collected near Panama City Beach. Of the three subspecies in the complex, subsp. *cruiseana* is the most isolated and the most distinct morphologically.

The second relatively homogeneous group of populations given subspecies status occurs in western Florida, Alabama, Mississippi, and eastern Louisiana on the outer coastal plain. Plants of this group, subsp. *hyssopifolia*, have the following set of characteristics: stems erect and unbranched from perennial bases and from basal rosettes produced at the ends of short to long lateral rhizomes or roots, stem leaves small and with ciliate margins (sometimes very linear), stems glabrate and often red-tinted, capitulescence subumbellate-cymose with one to a few heads, phyllaries glabrous and often spreading to recurved at the very tips. Only populations of such individuals occur in the western part of the distribution, but are sympatric with populations differing in inflorescence and habit in the most eastern part of the subspecies' range. Plants that are difficult to categorize as either subsp. *hyssopifolia* or subsp. *gossypina* are frequent in the Panama City Beach to Tallahassee corridor. The existence of these populations makes recognition of *hyssopifolia* as a species unsound.

The third subspecies includes the nomenclatural type of the species and is the most morphologically varied of the three sub-

species of *Chrysopsis gossypina*. As treated here subsp. *gossypina* includes individuals with glandular and non-glandular heads and individuals with woolly and glabrous heads. The reasons for treating some of these morphotypes at the formal level are discussed below.

Varieties were not recognized in any species of the genus in this revision. Varieties have been recognized in the genus in the past. Fernald (1937) treated *Chrysopsis floridana* as a variety of *C. mariana*. This was not found to be a reasonable classification, since the taxa differ in many morphological traits and even have different chromosome base numbers. Fernald also described a second variety of no significance in *C. mariana*, var. *macradenia*. Dress (1953) described a new variety in *C. scabrella*, but the name was never validly published. I have chosen not to give the morphotype Dress recognized any nomenclatural status. Dress also proposed that *C. gigantea* be treated as a variety of *C. hyssopifolia* (i.e. *C. linearifolia*), but this combination also was not published. Torrey and Gray (1842) treated *C. hyssopifolia* as a variety of *C. trichophylla*. Long (1970) treated *C. subulata* as a variety of *hyssopifolia* under the generic name *Heterotheca*. I have not accepted any of the relationships that these combinations imply and so none have been used in this revision.

Herbarium collections are not always helpful in assessing whether a morphotype should receive variety or form status. Generally, insufficient numbers of plants from a single population are collected to determine whether the population sampled consisted of only one morphotype or of several morphotypes. Following my usage of the terms "variety" and "form" this distinction is critical (Semple, 1974). For example, no population of *Chrysopsis godfreyi* studied in the field consisted of only the woolly-leaf form or the non-woolly, green leaf form (Semple, 1978a). Both morphotypes occurred in all populations and therefore were given the rank of form. Had both morphotypes existed in pure populations, they would have been given varietal status. The same distinction was found to be true of the densely glandular-headed individuals of *C. gossypina*. Godfrey (1949) treated these as f. *decumbens*. My field work supports Dr. Godfrey's conclusion.

The level at which to recognize Nuttall's *trichophylla* was the most troublesome aspect of the revision for several reasons. The first reason is the fact that nearly all previous authors have treated

the taxon as a species, but I quickly decided that it was not deserving of this rank. Second was the question of what rank it did deserve, if not species. Certainly the type specimen of *trichophylla* is different from the types of *hyssopifolia* and *gossypina* in leaf shape, pubescence, and capitulescence characteristics. Examination of many collections indicated that the type of *trichophylla* is part of a continuum of variation in leaf shape and pubescence. Phyllary shape also varies greatly and is not useful as a key characteristic. The type collection of *trichophylla* has a few large heads in a cymose capitulescence, acute erect to recurved phyllaries that are glabrous, leaves that are sparsely covered with long woolly hairs, peduncles that are glabrous, and an apparently erect habit. The collection was made in the "Carolinas" where plants with this combination of characteristics are rare. Such plants are more common in parts of Georgia and north-central and eastern Florida. Plants similar to this kind predominate in the Tallahassee to Panama City region of Florida, but these have coarse ciliate leaf margins, which is characteristic of subsp. *hyssopifolia*. The stem habit of all these *trichophylla*-like plants varies from erect and relatively unbranched to highly ramose and ascending to erect. In Georgia and South Carolina plants have been collected that are even more glabrous than the type of *trichophylla* and have very large heads with erect phyllaries. All these glabrous-headed plants could be assigned to a single species and have been by some authors (Small, 1903 & 1933; Harms, 1974; Radford et al., 1968). To do this, however, an arbitrary degree of pubescence has to be chosen to distinguish *C. trichophylla* from *C. gossypina*.

Each of the characteristic states that defines the *trichophylla* group is only one state in a continuum from one extreme condition to the opposite. Individuals have been collected that have one or more of the *trichophylla* traits in combination with *gossypina* traits. Plants having large heads with hairy and erect phyllaries have been collected in Florida and Georgia. Decumbent, but glabrous plants occur in the Carolinas. Peduncle pubescence varies greatly so that some plants have glabrous heads but woolly peduncles, while others have glabrous heads and glabrous peduncles. Still others have peduncles with a few hairs and are thus intermediate. The frequency of plants with a combination of some *trichophylla* characteristics and some *gossypina* or *hyssopifolia* characteristics is sufficiently high in the region where "pure" *trichophylla* plants have been collected that recognizing *trichophylla* as more than a form or

variety is unjustifiable. No arbitrary decision about the degree of hairiness was necessary to separate any of the $2n = 10$ and $2n = 8$ species. It would be inconsistent to adopt such an arbitrary limit in order to recognize species in the $2n = 18$ complex.

Nuttall's *trichophylla* could have been treated as either a variety or a form of one of the subspecies of *Chrysopsis gossypina*. The inclusion of the *trichophylla* morphotypes in either subsp. *cruiseana* or subsp. *hyssopifolia* would expand these taxa to useless limits. Furthermore, *trichophylla* morphotypes occur within the range of subsp. *gossypina*. Therefore, *trichophylla* is treated as part of subsp. *gossypina*, which has traditionally included many morphotypes.

The nature of population dynamics in *Chrysopsis* makes the choice of either variety or form rank for *trichophylla* possible. A large colony of plants can develop over a few seasons from the progeny of one or a few plants. Such populations tend to be composed of genetically similar individuals. Thus, "pure" populations of *trichophylla* morphotypes potentially could be encountered in South Carolina, Georgia, and Florida. These *trichophylla* populations would be sympatric in the broad sense with populations of *gossypina* morphotypes. Such populations are short lived and could be replaced by ones consisting of another kind of plant or intermediate ones. This pattern of distribution is the kind that I have suggested warrants varietal level status (Semple, 1974). I have chosen to minimize the nomenclatural importance of this particular glabrous-headed variant of *C. gossypina* because the importance of the variant has been given in the past is excessive. Treating the variant as f. *trichophylla* retains the name, but indicates that it is not significant at this time.

RELATIONSHIPS WITHIN CHRYSOPSIS

Sufficient data on the similarities and differences between the ten species of *Chrysopsis* are available that a phylogenetic history of the genus can be suggested at this time. Although much of what is stated must be speculative, the history takes into consideration all the information available. The hypothesized phylogenetic history of *Chrysopsis* given below is pictorially summarized in Fig. 3.

The ancestor of the genus is believed to have been an $x = 5$ taxon native to southwestern North America, possibly in the Texas-Mexico region. The range of this taxon later expanded eastward to Florida along the coastal plain, when conditions permitted. The

population complex became isolated in Florida, and the members evolved to a state recognisable as *Chrysopsis*. The fate of the more western populations is unknown. They may have given rise to other genera related to *Chrysopsis* such as *Xanthisma* and *Amphiachyris* or they may simply have gone extinct.

In Florida these early progenitors of the genus evolved the following set of characteristics: the $x = 5$ standard karyotype (Semple and Chinnappa, 1980a), a monocarpic to weakly perennial habit, woolly basal rosette leaves with flagelliform hairs (Semple, Blok, & Heiman, 1980), sessile and woolly stem leaves, a few-headed lax cymose capitulescence, densely stipitate glandular phyllaries and peduncles, and cypselas with a pappus of short outer bristles and long inner ones. The taxon retained the yellow ray color of its ancestor to the west. Also retained were the out-crossing breeding system and short taproot.

The ancestral populations were divided, perhaps by simple isolation, into two subgroups which were subjected to slightly different environmental conditions and which had different gene frequencies. In time different genes were fixed in each subgroup. New allelic forms of other genes evolved and were fixed in each set of populations, furthering divergence between the subgroups. Seed dispersal permitted exchange of some genes between populations within each subgroup, but not between subgroups. One subgroup is thought to have evolved the following set of characteristics: densely stipitate glandular peduncles and phyllaries, clasping stem leaves, and fruit without any distinct glandular ridges. From this first phylogenetic group with $x = 5$ evolved the $x = 4$ line following the processes described in Semple and Chinnappa (1980a & b). The second subgroup evolved the following different set of traits: glabrate peduncles and phyllaries, sessile and glabrous to sparsely woolly stem leaves, and fruit with one to many pronounced clavate, red-yellow translucent ridges. Once these two groups had evolved they again became sympatric in the northern Florida region.

Geographic isolation and subsequent adaptation to different habitats was apparently a recurrent pattern of evolution in the genus. This must have been particularly true in the case of *Chrysopsis pilosa*, the most divergent species in terms of morphology, chemistry, and cytology. The divergence is easily understood if the taxon had a long history of migration from the Florida region to the Ozark Plateau (Fig. 7E). If migration involved short steps by

ephemeral populations of a few individuals for much of the time, but with the occasional generation of large population size, such a situation would have favored genetic drift and would have led to speciation according to the Carson Founder-Flush Speciation Theory experimentally tested by Powell (1978). The effect of such boom-bust fluctuations in population size would have been to maximize the rate of divergence. Once in the drier regions of the Ozark Plateau, drier climatic conditions would have favored the evolution of the annual habit, since more changes in morphology would have been required for the species to become a true perennial utilizing a long taproot to overcome dry soil conditions at the end of the summer. A shift in flowering time from fall to early summer would have advantages as well because of the dry late summer conditions. In addition the lower chromosome number and reduced amount of chromatin in the karyotype could have resulted in an increase in growth rate permitting the plant to achieve flowering size more quickly (Semple & Chinnappa, 1980a). During this long process of specialization that resulted in the evolution of *C. pilosa*, some populations apparently became isolated and diverged in different ways. These populations are thought to have ultimately evolved into *Bradburia hirtella*, with a very rare $n = 4$ race and the common $n = 3$ race (Semple & Chinnappa, unpublished).

Geographic isolation appears to have been critical for speciation in both $x = 5$ phylogenetic lines. The stipitate-glandular group of species can be divided into two subgroups of two species each. One pair occupies the Florida peninsula and consists of the widespread mainland species *Chrysopsis scabrella* (Fig. 8F) and the Tampa Bay endemic *C. floridana* (Fig. 9F). The second species is known from less than a half dozen locations. These populations occur on isolated sandhills with Sand Pine communities. The other pair of species is found in the Florida panhandle region where both species have limited distributions. *Chrysopsis lanuginosa* occurs to the north and east of Panama City, occupying disturbed sites (Fig. 9F). Its range appears to have greatly expanded only recently with the onset of clear-cut logging operations in the area (R. K. Godfrey, personal communication). The second panhandle species, *C. godfreyi*, is endemic to the Gulf coast barrier islands from Panama City west to Alabama (Fig. 10F). Both panhandle species have long woolly hairs on the basal rosette leaves, clasping stem leaves, and large heads which nod in bud. Both peninsular species have short woolly hairs

on the basal rosette leaves and small heads erect in bud. The stem leaves of *C. floridana* are slightly clasping; those of *C. scabrella* are non-clasping.

Similarities in morphology between *Chrysopsis godfreyi* and *C. floridana* suggest that both evolved in response to similar environmental pressures. Individuals of both species are perennial. Both have a dense white woolly indument on the leaves and stems and both have a compact few-headed capitulescence. These traits may in some way be due to the barrier island habitat *C. godfreyi* now occupies and *C. floridana* may have originally occupied. The few populations of *C. floridana* may be relictual, the species having once been more common in the area when the sandhill habitats were the tops of barrier island sand dunes. In contrast both inland species (*C. lanuginosa* and *C. scabrella*) are usually biennial and have light green, densely stipitate-glandular stem leaves. Both have many-headed capitulescences that are very distinct from those of the other species of the region. The combination of capitulescence differences and leaf indument differences may facilitate distinction by foraging insects between the species in each regional pair. Floral color changes do not seem to have been available for this purpose, all the species of the genus being the same. Background and head positioning apparently were utilized in alternative.

The degree of difference is greater between *Chrysopsis floridana* and *C. scabrella* than between *C. godfreyi* and *C. lanuginosa*. The length of time each pair has existed may be responsible for this. The possible relictual distribution of *C. floridana* implies a long history for the species. Of course the greater difference between *C. floridana* and *C. scabrella* than between *C. godfreyi* and *C. lanuginosa* may also be due to simple chance and not reflect age at all.

In the second $x = 5$ line geographic isolation also apparently resulted in divergence and a move toward speciation. As in the stipitate-glandular group, the split in morphotypes is geographical and involves peninsular and panhandle populations. The two subspecies of *Chrysopsis linearifolia* differ in head size and capitulescence characteristics, as well as in leaf shape. When the two taxa were described (Semple, 1978b), the existence of plants of the subsp. *dressii* morphotype in the range of subsp. *linearifolia*, and vice versa was noted. Interestingly, these disparate individuals occur near the coast and generally in the region where the specialized species of the stipitate-glandular group occur. The history of these regions has apparently favored divergence in *Chrysopsis*.

Somewhere in northern Florida at some time in the past an individual with $n = 4$ and looking much like *Chrysopsis mariana* hybridized with an individual with $n = 5$ that looked similar to *C. linearifolia* subsp. *dressi* or *C. subulata*, but with nonsubulate phyllaries. From this hypothetical event evolved the $x = 9$ *gossypina* complex, which has been shown to be allopolyploid in nature (Semple & Chinnapa, 1980b). The hybrid origin of the complex indicates why so much morphological variation occurs within it. The distributions of these morphotypes have been mentioned briefly in the section on taxonomic units. The morphotypes have restricted and sometimes isolated distributions within the total range of *C. gossypina*.

Although not absolutely, *Chrysopsis gossypina* can be divided into a panhandle complex and a peninsular complex. Each complex extends outward on the coastal plain, westward and northeastward respectively. The panhandle complex is subdivided into semi-isolated groups of populations by several large rivers and estuary systems. Subsp. *cruiseana* occupies the barrier island region (Fig. 15C); typical subsp. *hyssopifolia* occupies the western mainland region; while the eastern region is occupied by individuals with characteristics of both subsp. *gossypina* and subsp. *hyssopifolia*. The ancestral hybridization event giving rise to the entire complex may have occurred in the eastern region surrounding Tallahassee. Both diploid *C. mariana* and *C. linearifolia* occur in this region.

Alternatively, the hybridization event yielding the $x = 9$ phylogenetic line could have taken place further east near Gainesville, Fla. In this region, diploid *Chrysopsis mariana* populations have been discovered. Also, in Alachua County there are populations of *C. subulata* that consist of plants with non-subulate phyllaries, but otherwise typical *subulata* morphology. *Chrysopsis gossypina* in this second area can be very similar to *C. subulata*, causing some difficulty in identification. When such a population of *C. subulata* was encountered during field work, plants were collected that appeared to be aberrant members of the species and this was later confirmed by the $2n = 10$ chromosome number obtained. At the site as well, a $2n = 14$ *C. subulata* \times *gossypina* subsp. *gossypina* individual was also collected. The similarity in the two species at this location in their respective distributions may be interpreted as 1) environmentally induced convergence, 2) chance, or 3) relictual, both species having retained very primitive morphotypes in this area. If the last situation is correct then perhaps *C. gossypina*

evolved in this region by hybridization between primitive morphotypes of *C. mariana* and *C. subulata*.

Within subsp. *gossypina* there occur several rather different morphotypes, which require some explanation about their origins. Since the species is of hybrid derivation, it includes genes from both the stipitate-glandular line and the translucent-ridged fruit line of evolution. It is postulated that depending upon the environmental conditions or simple chance, genes from only one parental line became fixed in some populations. In these populations the plants may even have backcrossed with one or the other of the parental taxa to further blur the distinctions. More likely, however, is the possibility that the morphological convergence toward one or the other parental line came about simply because essentially the same genes were present in the allopolyploid populations and the diploid populations in some cases. The subtle differences that occur between the diploid and mimicing allopolyploid morphotype are due possibly to the differences in chromosome number and the expression of some genes derived from the second parental line in the allopolyploid phenotype. In populations containing f. *decumbens* a single modifier gene could be determining whether an individual manifests the f. *gossypina* or the f. *decumbens* phenotype, as is perhaps the case with the forms of *Chrysopsis godfreyi*. The gene systems controlling the different morphologies could be quite complex, but their activation or suppression very simple. In the case of the *trichophylla* morphotype, the continuum between very glabrous and very woolly plants is such that a more complex genetic control system appears to be involved. Only rarely does a plant possess a full complement of genes that induces development of a pure *trichophylla* phenotype. That is, the *trichophylla* phenotype could be determined by a multi-allelic, multi-genic blended inheritance. Carefully controlled breeding studies need to be conducted to determine what genetic systems are involved in each of these cases.

The most difficult species to place phylogenetically is *Chrysopsis latisquamea*. It is the only species with luteolin in floral extracts in large enough quantities to be easily detected. This could be a relictual trait or one recently evolved. It has densely stipitate-glandular peduncles and phyllaries (characteristics of the *scabrella* group) and clavate translucent ridges on the fruit (characteristic of the *subulata* group). The origin of the species could thus be hybrid in nature. Or, it may represent an early offshoot of the $x = 5$ ridged-fruit phylogenetic line that differentiated before the line as a whole

lost the ability to produce densely stipitate-glandular structures. It is clearly not a part of the *gossypina* complex as Harms (1974b) suggested. Its $2n = 10$ chromosome number precludes this relationship. No evidence for hybridization with *C. gossypina* was found. *Chrysopsis gossypina* can hybridize with species in both $x = 5$ lines and with at least *C. pilosa* in the $x = 4$ line. There is no real reason to assume that it could not ever hybridize with *C. latisquamea* as well. The phylogenetic position of *C. latisquamea* is thus uncertain. In Figure 3 it is indicated with broken lines as arising from near the point at which the two $x = 5$ lines diverge.

In summary, evolution in *Chrysopsis* has proceeded in two main ways. First, changes in the karyotype have accompanied or brought about significant changes in morphology and distribution. Second, geographic isolation and small population size have apparently favored repeated divergence leading to speciation. The relative times of various events are unknown as is the age of the genus itself.

SYSTEMATIC TREATMENT

The following systematic treatment is based on field work during 1974–1978 and extensive herbarium studies on general and type collections. Specimens from the following herbaria were examined and annotated; DUKE, F, FSU, GA, GH, MT, NCSC, NY, OAC, PH, TENN, TEX, TUFTS, UNCC, US, USF, and WAT. Discussions of the morphology and the phylogeny of the genus have been presented in part in Semple (1977, 1978 a & b) and Semple et al. (1980), in which are also given location and voucher data of collections made as part of this study.

Chrysopsis (Nutt.) Ell., Sketch Bot. S.C. and Ga. 2: 333. 1824.
nomen conservandum.

Inula section *Chrysopsis* Nutt., Gen. North Amer. Pl. 2: 150, 1818. TYPE: *Inula mariana* L.

Diplopappus Cass., Soc. Phil. Bull. des Sc. 137. 1817. nom. ill.

Diplogon Raf., Amer. Monthly Mag. 2: 268. 1818. nom. rej.

Hefeldera Sch.-Bip. Flora 36: 35. 1853.

Heterotheca sect. *Chrysopsis* (Nutt.) Harms, Wrightia 4: 12. 1968. in part. sensu Harms, Castanea 39: 155–165. in full.

Plants annual, biennial, or perennial, herbaceous or suffrutescent. *Stems* erect, ascending, or decumbent, woolly pubescent to glabrous, or stipitate glandular. *Basal rosette leaves* spatulate to

oblanceolate, narrowing to petiole-like bases, sessile, entire or apically dentate-serrate, sparsely to densely woolly-pubescent, the hairs flagelliform, arachnoid-pubescent, or pilose. *Stem leaves* linear to ovate, elliptic, or lanceolate, sometimes clasping the stem, glabrous to densely short or long woolly-pubescent, or densely stipitate-glandular, pilose or arachnoid-pubescent, margins entire or obscurely dentate, sometimes coarsely ciliate. *Capitulescence* cymose, subumbellate-cymose, or cymose-paniculate; *heads* solitary in depaupered shoots to 100 or more in robust plants, showy, radiate, borne on nearly naked to leafy-bracted peduncles; *involucre*s campanulate, 5–12 mm high; *phyllaries* in 3–5 unequal series, 1-nerved, linear-lanceolate to oblanceolate, glabrous or variously pubescent, sometimes stipitate-glandular or sessile-glandular. *Ray florets* pistillate, 9–36, straps 5–15 mm long, yellow. *Disc florets* 5–8 mm long, ampilate, the throat making up about half the length, the lobes 0.5–1 mm long, yellow. *Fruit* a cypsela, body compressed-obconic, smooth or with 1–10 weak ribs and sometimes 1–4 yellow to red-brown, clavate, translucent ridges per side, sparsely to densely strigose, 1.5–3 mm long; *pappus* double, the outer bristles short, ca. 0.5 mm long, thin and barbellate to scale-like, the inner bristles thin, barbellate, 4–7 mm long. Chromosome base number: $x = 5$; derived bases $x = 4$ and 9.

The genus is distinguished by the following set of characteristics: basal rosette leaves with flagelliform hairs, florets yellow, ray and disc fruit similar, pappus double, the outer whorl of short bristles, the inner whorl of long ones, base number of $x = 5$ and derived bases of $x = 4$ and 9.

The general distribution of species groups, habit variation, and floret and trichome morphology of the genus are illustrated in Figs. 1, 4, and 5 respectively. The leaf anatomy of the genus was described in Semple et al (1980). It was undistinctive and similar to the leaf anatomy of species of *Heterotheca*, *Solidago*, and some species of the lower base number segregate genera of the *Haplopappus* complex.

There is considerable habit variation in *Chrysopsis*. The basic habit appears to be that possessed by *C. gossypina* subsp. *gossypina*, *C. godfreyi*, and *C. latisquamea* in part (Fig. 6A). A basal rosette develops the first season; a single shoot with branches ending in few-flowered cymose capitulescences develops the second season. The plant may produce additional basal rosettes from its lowest stem

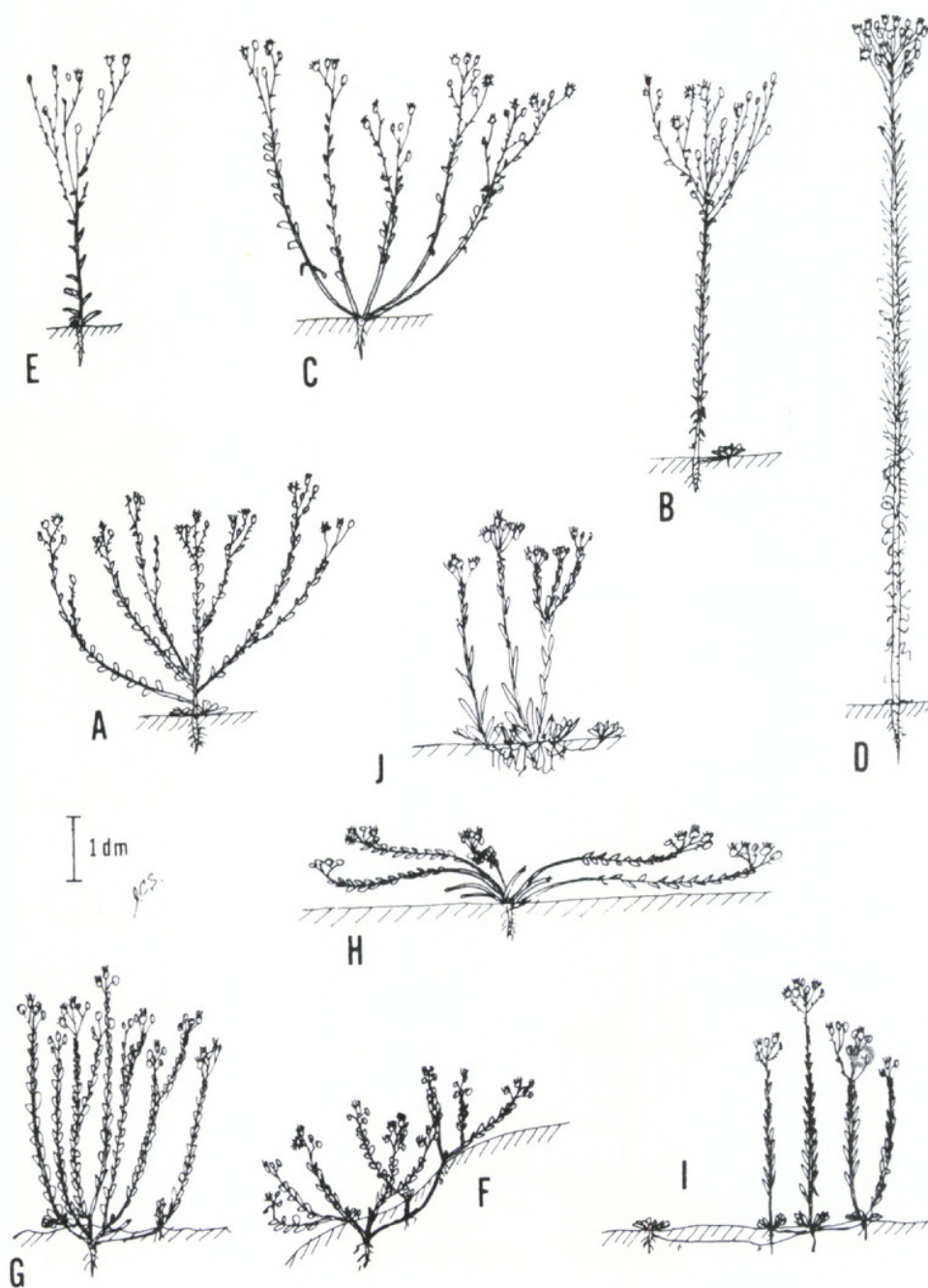


Figure 4. **Habit variation in *Chrysopsis*.** A full discussion is given in the text. All figures are at the same scale. A. *C. gossypina* subsp. *gossypina*, *C. godfreyi* and *C. latisquamea* (in part). B. *C. latisquamea* (in part) and *C. linearifolia* subsp. *dressii*. C. Appearance of damaged plants normally like (B) and plants blooming for the second time or more. D. *C. linearifolia* subsp. *linearifolia*. E. *C. pilosa*. F. *C. godfreyi* (in part). G. *C. floridana*. H. *C. gossypina* subsp. *cruiseana*. I. *C. gossypina* subsp. *hyssopifolia*. J. *C. mariana*.

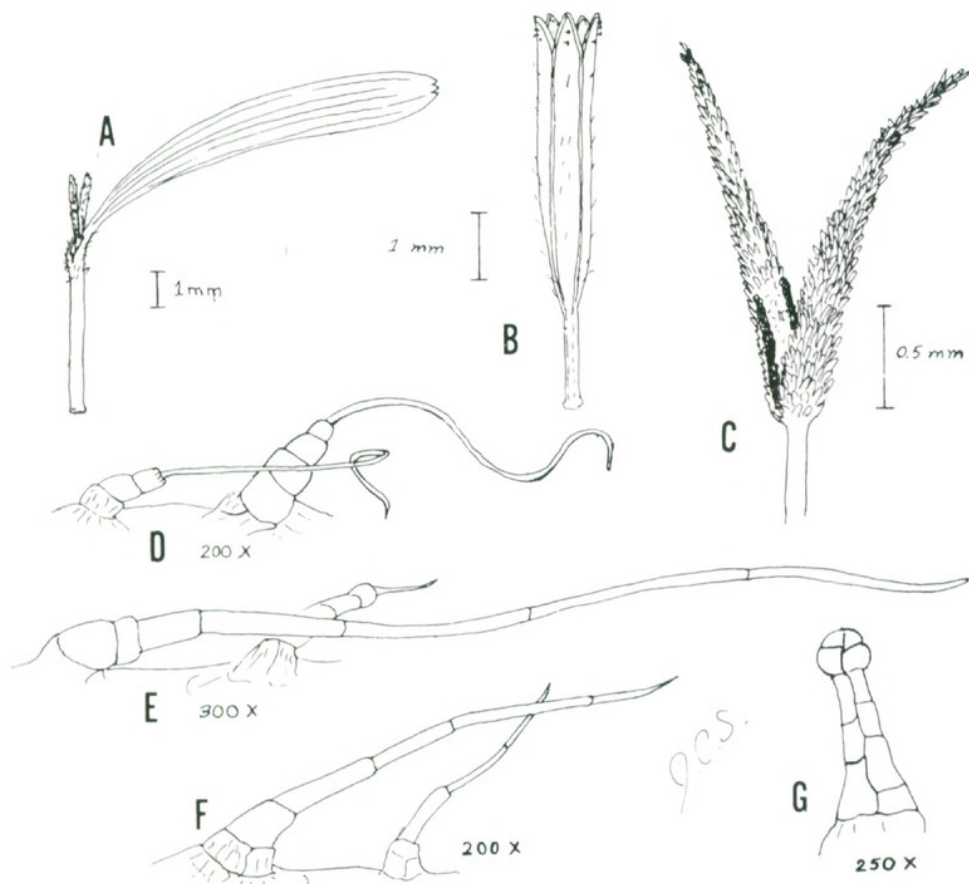


Figure 5. **Floral and trichome morphology in *Chrysopsis*.** A. Ray floret; hairs may be absent. B. Disc floret corolla; hairs and glands may be absent. C. Style branches of disc floret. D. Flagelliform hairs present in all species but two. E. Leaf hairs of *C. mariana*. F. Leaf hairs of *C. pilosa*. G. Stipitate glandular trichome. The size of the trichomes varies greatly even on the same tissue. A discussion of hair types and scanning electron micrographs of them were presented in Semple et al. (1980).

nodes or on short lateral rhizomes or roots. These permit the plant to survive another season. Greater apical dominance leads to growth forms with usually unbranched, erect stems (Fig. 6B) as found in *C. latisquamea* and *C. gossypina* subsp. *gossypina* in part, *C. scabrella*, and *C. linearifolia* subsp. *dressii*. Damaged plants and those perennating by production of additional secondary basal rosettes look like plants in Fig. 6C. Plants of *C. linearifolia* subsp. *linearifolia* can reach nearly two meters in height with up to 100 heads (Fig. 6D). Plants of *C. pilosa* are annual (Fig. 6E). Short and long lived perennial forms develop in several ways. Plants of *C. godfreyi* colonize dunes and can produce secondary basal rosettes at soil level, the lower portions of the older stems being buried in drifting sand (Fig. 6F). Plants of *C. floridana* are true perennials,

new growth arising from the bases of old shoots and at the ends of lateral rhizomes or roots (Fig. 6G). The shoots of *C. gossypina* subsp. *cruiseana* are decumbent and arise from old stem bases (Fig. 6H). The shoots of *C. gossypina* subsp. *hyssopifolia* arise singly from basal rosettes formed at the base of old stems and at the ends of long lateral rhizomes (Fig. 6I). Plants of *C. mariana* are true perennials, basal rosettes developing from a fibrous root system (Fig. 6J).

ARTIFICIAL KEY TO THE TAXA OF *CHRYSOPSIS* (NUTT.) ELL.

1. Fruits lacking yellow-red translucent ridges (in some forms of *C. gossypina* the ribs are distinct but not translucent); peduncles and phyllaries usually stipitate-glandular. 2.
2. Upper stem leaves stipitate-glandular, not woolly. 3.
3. Inflorescence open flat-topped corymbose; leaves linear-elliptic; phyllaries obtuse, short; stems erect; peninsular Florida; $n = 5$ (3) *C. scabrella*
3. Inflorescence compact corymbose or paniculate, buds nodding, leaves clasping stem. 4.
4. Inflorescence paniculate; phyllaries long attenuate, spreading to reflexed; leaves linear-lanceolate, stems erect often branching; central West Florida; $n = 5$ (5) *C. lanuginosa*
4. Inflorescence corymbose; phyllaries acute to attenuate; leaves lanceolate, sessile; stems procumbent to ascending; barrier islands of West Florida; $n = 5$ (6b) *C. godfreyi* f. *viridis*
2. Upper stem leaves glabrous to woolly, not densely stipitate-glandular. 5.
5. Upper leaves not usually greatly reduced, clasping auriculate; inflorescence subumbellate; stems ascending, perennial; Tampa Bay area only; $n = 5$ (4) *C. floridana*
5. Upper stem leaves reduced, long woolly or pilose or arachnoid. 6.
6. Upper leaves pilose or arachnoid (cobwebby hairs), not long woolly. 7.
7. Upper leaves pilose; inflorescence long peduncled, corymbose; erect annuals; Ozark Plateau west to Kansas and Texas, rare and perhaps introduced in states of the SE U.S.; $n = 4$ (2) *C. pilosa*

7. Leaves and portions of stem arachnoid pubescent; inflorescence subumbellate; fibrous rooted perennial; N.Y. to Fla. west to southern Ohio and eastern Texas; $n = 4, 8, 12, 16$ (1) *C. mariana*
6. Upper leaves woolly 8.
8. Inflorescence corymbose, buds nodding; procumbent to ascending stems; barrier islands of West Florida; $n = 5$ (6a) *C. godfreyi* f. *godfreyi*
8. Inflorescence cymose-corymbose, buds not nodding; procumbent stems; N.C. to Florida; $n = 9$ (10e) *C. gossypina* subsp. *gossypina* f. *decumbens*
1. Fruits with one or more translucent yellow-red ridges; peduncles and phyllaries not stipitate-glandular (except for *C. latisquamea*). 9.
9. Phyllaries stipitate-glandular, usually 1.5 mm wide or more; stems erect, branching; northern peninsular Florida; $n = 5$ (7) *C. latisquamea*
9. Phyllaries glabrous to woolly, not densely glandular, averaging 1 mm wide or less. 10.
10. Margins of upper stem leaves not pubescent; leaves linear-elliptic, linear-lanceolate, or linear, often glabrous. . 11.
11. Inflorescence subumbellate; leaves linear or linear elliptic. 12.
12. Leaves linear (more than 7 times long as wide); inflorescence usually many headed; stems erect, usually biennial; West Florida; $n = 5$ (8a) *C. linearifolia* subsp. *linearifolia*
12. Leaves linear-elliptic (less than 7 times long as wide); inflorescence few-headed; procumbent stems, perennial; barrier islands of West Florida; $n = 9$ (10a) *C. gossypina* subsp. *cruiseana*
11. Inflorescence open corymbose-cymose; leaves linear, linear-lanceolate to elliptic, often twisted; stems erect, usually biennial; central and southern peninsular Florida; $n = 5$ (8b) *C. linearifolia* subsp. *dressii*
10. Margins of stem leaves pubescent, surfaces glabrous to densely woolly; leaves elliptic, lanceolate, or linear. 13.
13. Phyllaries long subulate, often twisted, biennial to short lived perennials; central peninsular Florida; $n = 5$ (9) *C. subulata*

13. Phyllaries acute to attenuate, not long subulate
(*C. gossypina*) 14.
14. Inflorescence subumbellate; leaf margins distinctly
serrate-pilose; stems erect; usually perennial; La. to
central West Florida, and a few scattered locations
further east; $n = 9$
..... (10b) *C. gossypina* subsp. *hyssopifolia*
14. Inflorescence corymbose-cymose; leaf margins various
(*C. gossypina* subsp. *gossypina*). 15.
15. Upper stem leaves pilose to glabrous; margins pil-
ose; phyllaries glabrous; stems erect; N.C. to central
West Fla.; $n = 9$
(10d) *C. gossypina* subsp. *gossypina* f. *trichophylla*
15. Upper stem leave glabrous to densely long-woolly;
phyllaries glabrate to woolly; stems procumbent to
erect, biennial or perennial; Va. to Florida on
coastal plain; $n = 9$
(10c) *C. gossypina* subsp. *gossypina* f. *gossypina*

1. ***Chrysopsis mariana* (L.) Ell., Sketch Bot. S.C. and Ga. 2: 335. 1824.**

Inula mariana L. Sp. Pl. 2nd ed. 2:1240. 1763. TYPE: A specimen in the Linnean Herbarium labelled by Linnaeus as *Inula mariana* (not seen).

Inula glanulose Lam. Encycl. Meth. Bot. 3: 259. 1789.

Diplopappus marianus (L.) Cass. ex Hook Compan. to Bot. Mag. 1: 97. 1836.

Inula mariana L. var. Nutt. ex. DC. Prod. 5: 327. 1836, in syn.

Diplogon mariana (L.) Raf. ex DC. Prod. 5: 327. 1836, in syn.

Chrysopsis mariana (L.) Ell. var. *macradenia* Fern., Rhodora 39: 455. 1937.
TYPE: Virginia, 1 mil NW of Williamsburg, 19 Oct. 1920. Fernald & Long 6885 (HOLOTYPE,GH!; ISOTYPES,PH!; US!).

Chrysopsis mariana (L.) Ell. f. *efulgens* Fern., Rhodora 48: 60. 1946. TYPE: Virginia, NW of Newville, 13 Sept. 1945. Fernald & Long 14,996 (HOLOTYPE,GH!; ISOTYPES,NY!,US!,GH!).

Heterotheca mariana (L.) Shinnars, Field & Lab. 19: 71. 1951.

Plants perennial, new stems arising from basal rosettes borne on the fibrous rootstock or at the ends of short lateral rhizomes or roots. *Stems* erect or ascending, usually unbranched, 2–9 dm high, with long silky hairs that twist together at the ends, often purple-tinged. *Basal rosette leaves* spatulate to oblanceolate with petiole-like bases, to 25 cm long and 4 cm wide, obscurely dentate apically or entire, acute or obtuse, with long silky hairs like the stems,

becoming glabrate. *Stem leaves* reduced upward, sessile, lanceolate to elliptic oblong, 1–3 cm long, entire or obscurely dentate, acute, with hairs like the basal leaves or glabrate and ciliate marginally. *Capitulescence* usually crowded subumbellate-cymose with 1–50 or more heads depending upon the robustness of the plant; *peduncles* densely stipitate-glandular, the glandular tips yellow to brown, 1–5 cm long, sometimes with a few bracteoles, arising from the axes of the upper-most stem leaves or in the axes of peduncular bracteoles. *Involucres* campanulate, 7–10 mm high (ploidy-level-dependent, in part); *phyllaries* in 4–5 unequal series, erect, linear \pm 1 mm wide, acute, densely stipitate-glandular on the outer surfaces. *Ray florets* 10–22, averaging 14 per head, the strap 8–11 mm long, 2–3 mm wide. *Disc florets* 5–7 mm long, lobes 0.5 mm long. *Cypselas* straw to purple in color, short strigose, surface shallowly ribbed or smooth, 2–3 mm long; *pappus* double, the outer bristles short, the inner bristles 4–6 mm long. *Chromosome numbers*: $n = 4, 8, 12, 16$.

The species is easily recognized by its capitulescence and leaf pubescence. The morphology and distribution are illustrated in Figs. 4J and 6A–E. The fruit is like that of *Chrysopsis floridana* illustrated in Fig. 9D. None of the variants described by other authors have been accepted as meaningful. Gland color was found to vary continuously from yellow to dark brown by Dress (1953). He placed Fernald's var. *macradenia*, distinguished by dark glands, in synonymy, as was done here for the same reasons. Dress (1953) also noted that the rayless condition of f. *efulgens* Fern. was due to insect damage and that even the type collection had some ray florets present, though partially eaten. Some differences in size can be attributed to ploidy level, while other times the differences are due to growth conditions.

The species inhabits open or partially shaded, disturbed sandy and clay soils of pine and oak woods, roadside embankments and natural rocky slopes. Diploid, tetraploid, and octaploid plants are confined to Florida. Hexaploid plants occur in Florida and extend the range to Long Island, New York, and Ohio in the north and extreme eastern Texas in the west.

Plants bloom on a north to south gradient from late August and September on Long Island to November and December in Florida. Occasionally plants may bloom in the late Spring in Florida.

REPRESENTATIVE SPECIMENS. **Alabama.** BALDWIN CO., Gateswood, Tracy 8,575 (GH, NY, US); CULLMAN CO., Cullman, Eggert s.n. (NY, US); ESCAMBIA CO., Atmore, Blanton

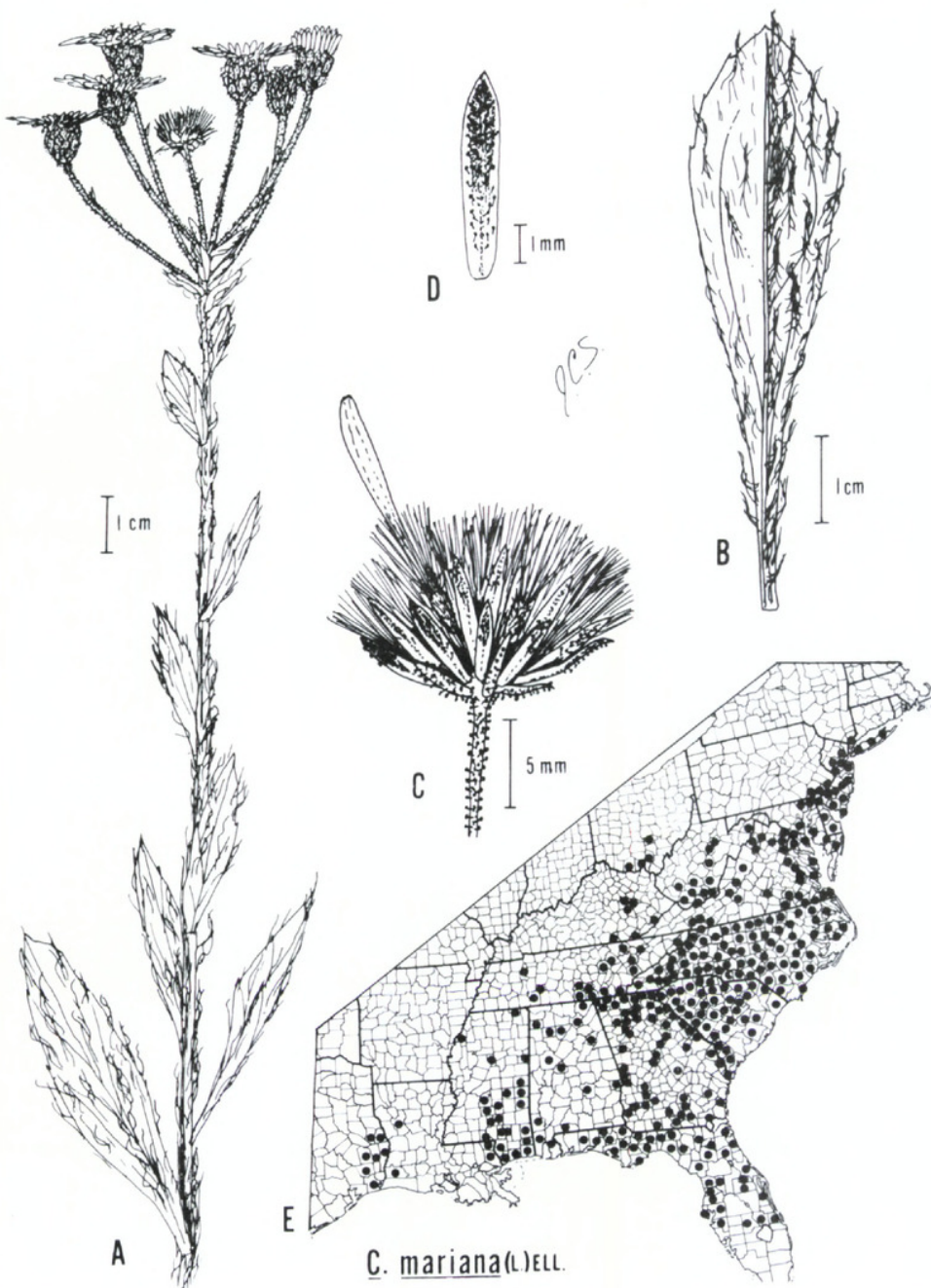


Figure 6. The morphology and distribution of *C. mariana*. A. Flowering shoot, the height and number of heads may be considerably greater than shown. B. Lower stem/basal rosette leaf; the cobwebby hairs are only shown as dense on one side. C. A dried head with only one ray floret shown. D. Mid series phyllary. E. County dot map of the distribution based on all collections seen and literature reports.

7,082 (GH); JACKSON CO., Bryant *Porter s.n.* (GH), MARSHALL CO., Albertville, *Biltmore Herb.* 165 (US); MONTGOMERY CO., Montgomery, *Eggleston* 5,139 (GH, NY). **Delaware.** KENT CO., Milford, *Goodale* 62,532 (GH); NEWCASTLE CO., Wilmington, *Tatnall s.n.* (GH); SUSSEX CO., Ellendale, *Tatnall* 194 (GH). **Florida.** ALACHUA CO., W. of Gainesville, *D'Arcy* 2,219 (GH, NY). BRADFORD CO., Starke, *Gilbert s.n.* (GH); BREVARD CO., N. of Wilson's Corner, *Shuey s.n.* (USF); COLUMBIA CO., Lake City, *Straub* 1 (GH); DUVAL CO., Jacksonville, *Curtiss* 5,317 (NY,US); FRANKLIN CO., Apalachicola, *Chapman s.n.* (GH,US); *Jones* 103 (US); HIGHLANDS CO., S of Lake Istokpoga, *Brass* 15,716 (US); HILLSBOROUGH CO., N of Branchton, *Lakela* 24,732 (GH,USF); MANATEE CO., Bradenton, *Tracy* 7,141 (GH,NY,US); OKEECHOBEE CO., Ft. Bassinger to Okeechobee City, *Small & DeWinkler s.n.* (NY); ORANGE CO., Clarcona, *Meislahn* 145 (US); PASCO CO., New Port Richey, *Carpernter s.n.* (GH); PINELLAS CO., N.E. of Clearwater, *Genelle & Fleming* 379 (USF); POLK CO., T. Meade, *Jennings s.n.* (USF); ST. JOHNS CO., W. of Hastings, *Ward* 2,278 (GH,US,USF); ST. LUCIE CO., Vero, *Small & De Winkler* 9,738 (GH,NY,US); VOLUSIA CO., Merritt's Is. Nat'l Wildlife Refuge, *Poppleton* 579 (USF); WAKULLA CO., N of Sopchoppy, *Godfrey* 55,217 (USF).

Georgia. CHARLTON CO., Folkston, *Harper* 670 (GH,NY); DAWSON CO., Amicalala Falls, *Duncan* 4,246 (CH); EFFINGHAM CO., 4 mi. from Clio, *Boole* 1,037 (GH); ELBERT CO., SE of Elberton, *Duncan* 10,573 (GH); GLYNNE CO., N of Brunswick, *Moldenke* 5,200 (NY); HARRIS CO., F.D.R. State Park, *Jones* 21,612 (GH); JACKSON CO., 11 Mi N of Athens, *Cronquist* 4,737 (GH,NY,US); PUTNAM CO., S of Madison, *Cronquist* 4,854 (GH,NY,US); RICHMOND CO., Augusta, *Cuthbert* 314 (NY); SUMTER CO., Leslie, *Harper* 1,715 (GH,NY,US); UNION CO., N of Cooper Gap, *Duncan* 2,924 (GH). WALKER CO., N of Maddox Gap, *Cronquist* 4,811 (GH,NY,US). **Kentucky.** BELL CO., Pine Mt. *Kearney* 427 (NY); HARLAN CO., Pine Mt., *Kearney* 266 (GH,US); LEE CO., near Beattyville, *Braun* 2,148 (US); LETCHA CO., Pine Mt., *Braun* 295 (US); MCCREARY CO., Starns Park, *Rogers* 1,074 (US); POWELL CO., Natural Bridge, *McFarland* 2,042 (GH); WOLFE CO., Sky Bridge, *Braun* 2,065 (US). **Louisiana.** CALCASIEU PARISH, W of Sulfur, *Brown et al.* 8,623 (GH); NATCHITOCHES PARISH, Natchitoches, *Palmer* 8,798 (NY,US); ST. TAMMANY PARISH, Covington, *Arsene* 11,122 (US); WASHINGTON PARISH, W of Bogalusa, *Brown* 6,742 (GH). **Maryland.** ANNE ARUNDEL CO., SE of Leon, *Shull* 268 (GH,NY,US); CALVERT CO., Chesapeake Beach, *Hunnewell* 5,552 (GH); CECIL CO., Old Neck, *Abbott* 139 (US); HOWARD CO., W of Waterloo, *Wilkins* 3,052 (UNCC); PRINCE GEORGES CO., Hyattsville, *House* 197 (NY); WORCESTER CO., Snow Hill, *Moldenke* 6,596 (NY).

Mississippi. CLARKE CO., Shubuta, *Schuchert s.n.* (US); COVINGTON CO., Ora, *Tracy* 8,577 (GH,NY,US); HANCOCK CO., Kiln, *Demaree* 36,298 (NY); HARRISON CO., Biloxi, *Tracy* 4,773 (GH,NY,US). **New Jersey.** ATLANTIC CO., Humminton, *Gershey* 687 (GH); BURLINGTON CO., Atison, *Allen s.n.* (GH); CAMDEN CO., Parkdale, *Pennell* 9,118 (NY); CAPE MAY CO., Clermont, *Moldenke* 29,008 (US); GLOUCESTER CO., Newfield, *Tiedestrom* 8,065 (GH); MONMOUTH CO., Bradley Beach, *Pennell* 6,578 (NY); OCEAN CO., Lakewood, *Hunnewell* 6,979 (GH). **New York.** BRONX CO., near N Y Botanical Garden, *Gilly* 193 (NY); BURLINGTON CO., New Egypt, *Taylor* 2,675 (NY); RICHMOND CO., Staten Is., *Britton s.n.* (GH); SUFFOLK CO., Long Is., Naragansett, *Taylor* 1,506 (NY). **North Carolina.** BENTIE CO., Windsor, *Godfrey* 6,997 (GH); CASWELL CO., Yanceyville, *Godfrey* 5,549 (GH); CRAVEN CO., Fort Barnwell, *Godfrey & White* 6,834 (GH); FORSYTH CO., *Schallert s.n.* (NY). HAYWOOD CO., Waynesville, *Standley* 5,752 (US); JOHNSTON CO., SE of Smithfield, *Godfrey & Fox* 12,044 (GH); MACON CO., Highlands, *Magee s.n.* (GH); MCDOWELL CO., *Beaman* 214 (NY); MECKLENBURG CO., Charlotte, *Gress s.n.* (US); ORANGE CO., Chapel Hill, *Godfrey* 12,007 (GH); PAMLICO

CO., Grantsboro, *Godfrey & White* 6,827 (GH); ROWAN CO., Salisbury, *Heller* 83 (NY); RUTHERFORD CO., Chimney Rock, *Hunnewell* 10,038 (GH); SWAIN CO., S of Lauada, *Radford* 17,284 (US); TRANSYLVANIA CO., Frying Pan Gap, *Rydberg* 9,508 (NY); WAKE CO., Raleigh, *Ashe* 2,410 (NY).

Ohio. ADAMS CO., Shawnee State Forest, *Braun s.n.* (US); JACKSON CO., Liberty Twp., *Cronquist* 4,023 (NY); SCIOTO CO., Camp Gordon, CCC, Shawnee Forest, *Demaree* 11,130 (GH,NY). **Pennsylvania** CHESTER CO., Nottingham, *Pennell* 8,892 (NY); DELAWARE CO., Lansdowne, *Redfield* 2,979 (MO); LANCASTER CO., Pleasant Grove, *Small s.n.* (NY); PHILADELPHIA CO., Wissahickon Ravine, *Lang* 586 (GH); YORK CO., E of Bryansville, *Wherry s.n.* (PH). **South Carolina.** AIKEN CO., Aiken, *Ravenel s.n.* (US); BEAUFORT CO., Beaufort, *Millichamp* 418 (US); CHARLESTON CO., S of Charleston, *Moldenke* 5,176 (NY); FAIRFIELD CO., NE of Winnsboro, *Bell* 9,936 (GH); HORRY CO., near Burgess, *Weatherby* 7,132 (GH,US); JASPER CO., Savannah National Wildlife Refuge, *Mellinger s.n.* (GH); LEXINGTON CO., Batesburg, *McGregor* 73 (US); PICKENS CO., Clemson College, *House* 2,884 (NY,US). WILLIAMSBURG CO., Benson, *McCullough* 15 (US). **Tennessee.** CARTER CO., Roan Mt. Station, *Rydberg* 8,228 (NY); CUMBERLAND CO., E of Crossville, *Svenson* 4,187 (GH); FENTRESS CO., Allardt, *Shanks* 3,093 (GH); HAMILTON CO., Lookout Mt., *Vasey s.n.* (NY); KNOX CO., Knoxville, *Ruth* 3,784 (NY); MONROE CO., Cherokee National Forest, *Shanks s.n.* (TENN); SEVIER CO., Gatlinburg, *Miller* 2,224 (US); WAYNE CO., Natchez Trace Parkway, *McDougall* 1,099 (US).

Texas. JASPER CO., NW of Jasper, *Correll* 26,724 (GH). **Virginia.** AUGUSTA CO., Augusta Springs, *Stelle s.n.* (US); BEDFORD CO., *Curtis s.n.* (GH); BRUNSWICK CO., W of Triplett, *Fernald & Lewis* 14,509 (GH); CAROLINA CO., NE of Ruther Glen, *Ilitis* 2,341 (US); CARROLL CO., Galax, *Moldenke* 19,267 (NY); DINWIDDIE CO., S of Petersburg, *Fernald et al.* 15,371 (GH,NY,US); FAUQUIER CO., Hopewell Gap, *Allard* 932 (GH,NY); HANOVER CO., Ashland, *Chalmot s.n.* (US); HENRICO CO., Richmond, *Moorman* 3,001 (GH); MONTGOMERY CO., W of Blacksburg, *Kral* 11,435 (USF); NORFOLK CO., Norfolk, *Jensen s.n.* (GH,NY,US); PAGE CO., Luray, *Ball s.n.* (US); PRINCE EDWARD CO., Worsham, *Baldwin* 5,395 (GH); PRINCESS ANNE CO., W of Kempsville, *Kral* 14,357 (USF); SHENANDOAH CO., Massanutten, *Hunnewell* 11,357 (GH); SUSSEX CO., NW of Waverly, *Fernald & Long* 14,997 (GH); WARREN CO., Little Passage Cr., *Miller s.n.* (US). **West Virginia.** BARBOUR CO., Tygart Junction, *Greenman* 321 (GH); FAYETTE CO., *Nuttall s.n.* (GH); GREENBRIAR CO., White Sulfur Springs, *Mackenzie* 405 (NY); HAMPSHIRE CO., Capon Springs, *Core s.n.* (NY); MONROE CO., Sweet Springs, *Steele* 312 (GH,NY,US); SUMMERS CO., Bangers Springs, *Fox* 1,955 (GH); UPSHUR CO., *Dickey* 155 (GH).

2. *Chrysopsis pilosa* Nutt., J. Acad. Sci. Phila. 7: 66–67. 1834.

TYPE: The grassy plains of the Arkansas, *Nuttall s.n.* (HOLOTYPE, PH!; ISOTYPE, ? GH).

Not *Chrysopsis pilosa* (Walt). Britt., Mem. Torrey Bot. Club 5: 316. 1894.

Chrysopsis nuttallii Britt. Mem. Torr. Bot. Club 5:316. 1894.

Diplogon nuttallianum (Britt.) Kuntze, Rev. Gen. 1:334. 1891.

Heterotheca pilosa (Nutt.) Shinnery, Field & Lab. 19:68. 1951.

Plants annual, usually only one stem arising from the basal rosette that develops during the Spring. *Stems* erect, sparsely to densely pilose, 1.5–8 dm tall. *Basal leaves* oblanceolate narrowing to petiole-like bases, 5–10 cm long, 1–2.5 cm wide, pilose on both surfaces, entire to apically dentate, acute. *Stem leaves* reduced upward to 1 cm long or less, linear-elliptic, sessile, pilose, obscurely dentate or entire. *Capitulescence* lax cymose, the heads borne on branches arising from the upper most stem leaf axes and from the axes of leaves on primary and secondary branches; *peduncles* 1.5–7 cm long, short pilose, sometimes stipitate-glandular near the heads. *Involucres* campanulate, 6–9 mm high; *phyllaries* in 3–4 unequal series, linear, scarious marginally, sparsely glandular, sparsely to densely short to long pilose. *Ray florets* 11–24, averaging 16 per head, strap 7–10 mm long, 1–2 mm wide. *Disc florets* 4.5–6 mm long, lobes 0.5 mm long. *Cypselas* straw to brown in color, short strigose, smooth or slightly ribbed; *pappus* double, the outer bristles scale-like and short, the inner bristles 5–6 mm long. *Chromosome number*: $n = 4$.

The morphology and distribution of *Chrysopsis pilosa* are illustrated in Figs. 4E and 7A–E. The fruit is like that of *C. floridana* illustrated in Fig. 9D, but less strigose and the outer pappus bristles are broad and scale-like. The size and number of heads borne by a plant depends upon growth conditions. In drier regions and seasons the plants are typically small, few headed, and most stem leaves drop off quickly. The lower stem leaves persist to late in the season only under very moist conditions.

The species inhabits open areas in oak woods in the eastern part of its range and disturbed roadside margins and lots throughout. In the west it inhabits grassy areas in oak savanahs and patches of prairie. Its distribution in Tennessee and Mississippi may be relictual from drier times or may be due to more recent chance introductions along roadsides. The collections from North Carolina are most likely from chance introductions. Efforts to locate populations in central North Carolina during September of 1977 were unsuccessful and they may now be extinct. Soils vary from coarse sand and gravel to fine silt and clay types.

Plants come into bloom in May and continue blooming in some areas until October. The peak blooming period is June.

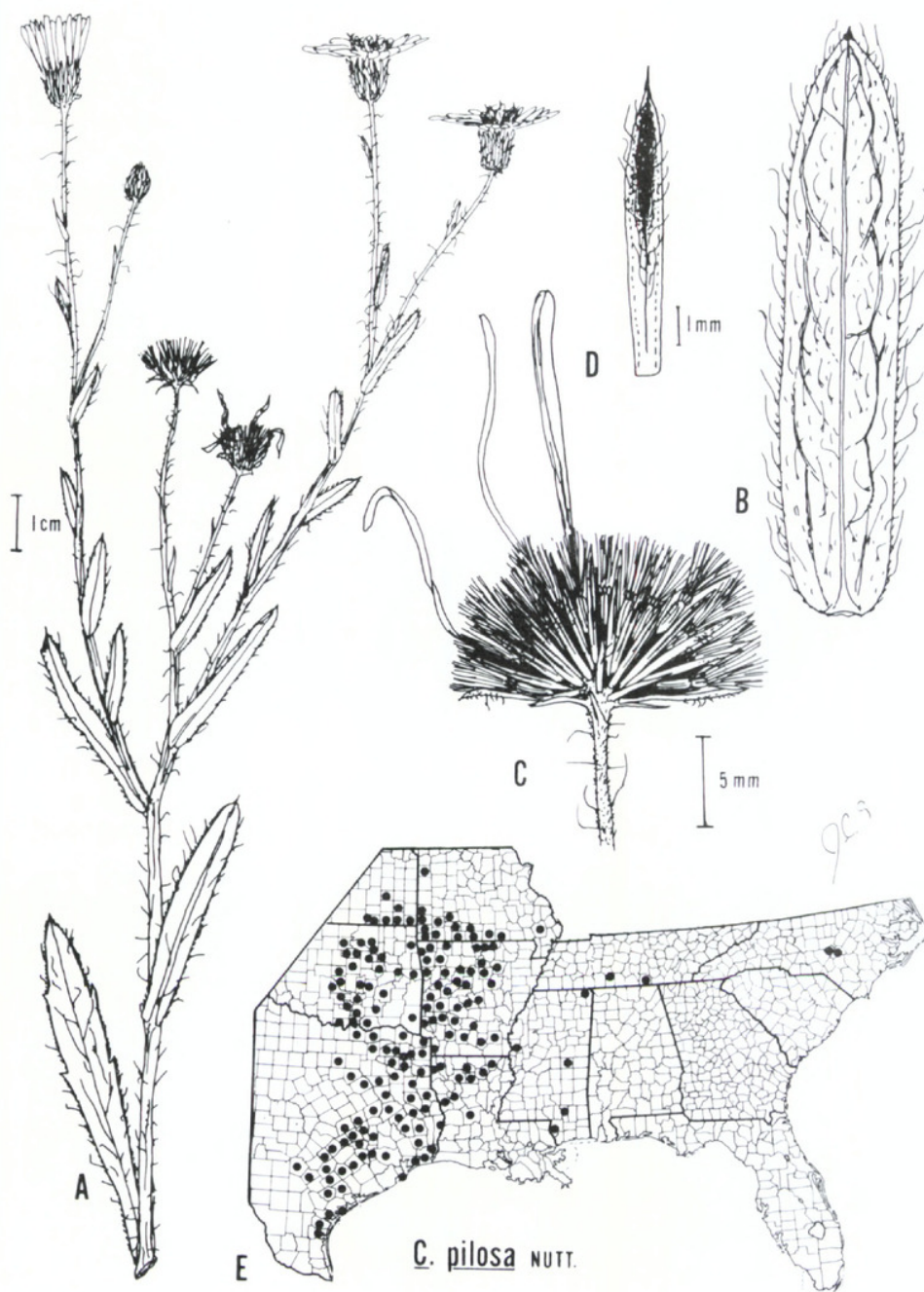


Figure 7. The morphology and distribution of *C. pilosa*. A. Upper portion of a flowering shoot with a few heads. Additional branches bearing heads can arise from lower stem leaves and from the axes of leaves of the inflorescence branches. B. Mid stem leaf; upper surface on the left, lower on the right, scale same as C. C. Dried head with a few ray florets drawn. D. Mid series phyllary. E. County dot map of the distribution based on all the collections seen.

REPRESENTATIVE SPECIMENS. **Arkansas.** BENTON CO., Siloam Springs, *Demaree* 22,396 (NY); BOONE CO., Harrison, *Palmer* 43,849 (NY); CAROLL CO., Busch 6,034 (UNCC); CLARK CO., Gordon, *Demaree* 40,492 (GH); CONWAY CO., Morrilton, Petit Jean State Park *Demaree* 25,223 (GH); DREW CO., 9 mi N of Monticello, *Demaree* 13,545 (US); FRANKLIN CO., 4 mi S of Ozark on Hwy 23, *Redfern* 17,304 (UNCC); FULTON CO., Salem, *Demaree* 26,321 (PH); GARLAND CO., Ouchita Mts. near Hot Springs, *Chase* 9,913 (NY, UNCC); HOWARD CO., Mineral Springs, *Demaree* 42,747 (GH); INDEPENDENCE CO., US Hwy 167 4 mi N of Beltsville, *Thomas* 16,367 (UNCC); JOHNSON CO., 5.4 mi S of Ozone, *Smith* 947 (UNCC); LOGAN CO., Booneville, *Demaree* 8,105 (GH,US); MADISON CO., 2 mi E of Wesley, *Carter* 18 (UNCC). MONTGOMERY CO., Hopper, *Tucker* 5,284 (UNCC); MILLER CO., Texarkana, *Eggert s.n.* (NY,US); NEVADA CO., 4 mi SE of Prescott Woods, *Hollister* 98 (US); OUACHITA CO., Beardon, *Demaree* 37,631 (GH); PIKE CO., Lake Greeson, *Tucker* 5,687 (UNCC); POLK CO., 6 mi E of Mena, *McWilliam* 545 (GH); POPE CO., Dover, *Demaree* 19,817 (NY); PULASKI CO., N of Little Rock, *Merrill* 506 (GH); SALINE CO., Bauxite, *Demaree* 34,247 (GH, UNCC); SCOTT CO., Mansfield, *Demaree* 18,173 (NY); SEVIER CO., 5 mi E of Lockesburg, *Tucker* 5,661 (UNCC); STONE CO., Big Springs, *Demaree* 59,378 (UNCC); VAN BUREN CO., 1 mi NE of Pee Dee, *Redfern* 29,402 (UNCC); WASHINGTON CO., Fayetteville, *Demaree* 22,428 (GH,NY). **Kansas.** CHAUTAUQUA CO., 3 mi NE of Sedan, *McGregor* 15,817 (GH); LABETTE CO., SW of Parsons, *McGregor* 4,452 (GH); MONTGOMERY CO., Dearing, *Gates* 21,632 (NY). NEOSHO CO., Chanute, *Boden* 7,035 (NY); WOODSON CO., *Lathrop* 1,558 (GH,NY). **Louisiana.** BOSSIER PARISH; Barksdale AFB, *Balogh* 152 (UNCC); CADDO PARISH, 2 mi NE of Mooringsgart, *Thieret* 21,174 (UNCC), 5 mi NW of Shreveport, *Correll* 10,100 (GH); LINCOLN PARISH, Douglas, *Moore* 5,225 (GH); MOREHOUSE PARISH, 6.5 mi NW of Beckman, *Thieret* 20,376 (UNCC); NATCHITOCHE PARISH, Chopin, *Palmer* 8,826 (NY,US); OUCHITA PARISH, W of West Monroe, *Thomas* 18,868 (UNCC); SABINE PARISH, Toledo Bend Lake, *Soarbrough s.n.* (UNCC); WEBSTER PARISH, Miden, *Brown* 5,341 (GH). **Missouri.** GREENE CO., Malden, *Bush* 166 (GH); HOWELL CO., 5 mi W of Plains, *Thomas* 9,925 (TENN); JASPER CO., Smithfield, *Palmer* 16,300 (GH); LAWRENCE CO., ¼ mi E of Spring River on Hwy 60, *Redfern* 24,888 (UNCC). **Mississippi.** FOREST CO., Hattiesburg, *Rogers* 6,841 (GH); TISHOMINGO CO., *Coleman* 50,644 (TENN); WASHINGTON CO., Greenville, *Sargent s.n.* (NY). **North Carolina.** HARNETT CO., 3 mi SW of Kipling, *Godfrey & Fox* 49,428 (GH,NY). **Oklahoma** ATOKA CO., 3.2 mi E of Waganoka, *Wiseman & Williams* 4 (UNCC); CLEVELAND CO., E of Norman, *Massey* 2,295 (UNCC); CREEK CO., W of Sapulpa, *Pennell* 5,394 (PH); HUGHES CO., Calvin, *Demaree* 12,728 (NY); JOHNSTON CO., Reagen, *Robbins* 2,623 (NY); LOVE CO., 2 mi SW of Bomar, *Goodman* 5,706 (GH); MARSHALL CO., 2.8 mi SW of Willis, *William* 469 (UNCC); MCCURTAIN CO., N of Tom, *Waterfall* 8,469 (GH); MCFAIN CO., SW of Norman, *Massey & Hoisington* 1,478 (UNCC); MURRAY CO., Platt Park *Merrill & Hagen* 949 (US); OKLAHOMA CO., W of Oklahoma City, *Waterfall* 768 (GH); OSAGE CO., Tulsa, *Ward* 16 (US); PITTSBURG CO., McAlester, *Palmer* 6,408 (US); PONTOTOC CO., Ada, *Robbins* 2,226 (NY). **Tennessee.** LAWRENCE CO., SSW of Summerton, *Kral* 48,412 (GH, US). **Texas.** ANGELINA CO., S of Lavalla, *Cory* 49,751 (GH, NY); ARANSAS CO., Aransas Refuge, *Cory* 45,763 (GH, NY, US); ATASCOSA CO., S of San Antonio, *Schulz* 417 (US); BASTROP CO., Bastrop-Buescher State Park, *Lundell* 8,979 (GH); COLORADO CO., Columbus, *Rushby s.n.* (NY); GALVESTON CO., Galveston Island, *Ridell s.n.* (US); GRAYSON CO., S of Gordonville, *Correll* 33,627 (GH); GREGG CO., Kilgore, *Barkley* 13,373 (NY); GRIMES CO., W of Roans Prairie, *Thomas & Brett* 4,422

(TENN); HARRIS CO., Houston, *Armon* 7,365 (GH); LAVACA CO., SE of Yoakum, *Tharp et al.* 49,175 (US); LEON CO., Centreville, *Corell* 33,987 (GH); MONTGOMERY CO., E of Conroe, *Raven & Gregory* 19,441 (US); MORRIS CO., SE of Daingerfield, *Cory* 56,944 (US); NACOGDOCHES CO., Cushing, *Tharp & Braun* 53-9 (UNCC); RUSK CO., NW of Tatum, *Cory* 56,461 (US); SAN AUGUSTINE CO., San Augustine, *Palmer* 10,615 (US); SELBY CO., Center, *Correll* 15,357 (UNCC); SMITH CO., NE of Tyler-Camp, *Moore* 519 (GH); TARRANT CO., S of Benton, *Whitehouse* 16,422 (NY, US); TRINITY CO., SW of Trinity, *Cory* 10,480 (GH); VICTORIA CO., E of Aloe, *Pennell* 5,498 (NY); WALLER CO., Hempstead, *Haab s.n.* (US).

3. *Chrysopsis scabrella* T. & G., Fl. North Amer. 2: 255. 1842.

TYPE: Florida, in pine woods, *Leavenworth s.n.* (HOLOTYPE, NY!, Torrey Herbarium; ISOTYPE?, GH, fragmentary).

Diplogon scabrellum (T. & G.) Kuntze, Rev. Gen. 334. 1891.

Heterotheca scabrella (T. & G.) Harms, Castanea 39: 162. 1974.

Plants biennial, rarely perennating a season or two more by production of one or more basal rosettes at the lower stem nodes, usually only one shoot arising from the basal rosette. *Stems* erect, or ascending if more than one, 4–10 dm tall, unbranched in the lower 2/3 or more, branches part of the inflorescence, woolly basally, stipitate-glandular above. *Basal rosette leaves* oblanceolate, sessile, apically dentate-serrate, 4–10 cm long, 1–2 cm wide, densely short-woolly on both surfaces, the hairs flagelliform. *Stem leaves* reduced upward, sessile, linear-elliptic, acute, densely stipitate-glandular on both surfaces, rarely the lower and mid stem leaves woolly. *Capitulescence* corymbose- cymose, 10–100 heads, usually congested and making up less than ¼ of the plant height; *peduncles* 2–10 cm long, stipitate-glandular, with a few linear, stipitate-glandular bracteoles. *Involucre*s campanulate, 6–9 mm high; *phyllaries* in 4–5 unequal series, linear, densely stipitate- glandular, 1 mm wide. *Ray florets* 19–32, averaging 21 per head, the strap 6–8 mm long, 1.5–2.5 mm wide. *Disc florets* 5–7 mm long, lobes 0.5–1 mm long. *Cypselas* straw to brown in color, short-strigose, smooth to shallowly ribbed, 2–3 mm long; *pappus* double, the outer bristles short, the inner bristles 5–7 mm long. *Chromosome number*: $n = 5$.

The morphology and distribution of *Chrysopsis scabrella* are illustrated in Figs. 4B and C and 8A–F. The plants have a yellowish-green color in the field that is not always retained upon drying. The species is distinguished by its many-headed, corymbose capitulescence and its small stipitate-glandular stem leaves. Dress (1953)



Figure 8. **The morphology and distribution of *C. scabrella*.** A. A moderate sized shoot with corymbose capitulescence. B. A bolting basal rosette with only the lower portion of the stem shown, scale same as A. The leaves are densely short-woolly pubescent. C. Mid stem leaf with glands only illustrated on one half. D. Dried head with only a few ray florets illustrated, scale same as C. E. Mid series phyllary. F. County dot map of the distribution based on all collections seen.

treated plants with woolly stem leaves as a variety, but the name was never published. I have found that the point at which leaf indument shifts from woolly pubescence to stipitate-glandularity varies from very low on the stem to more than $\frac{1}{2}$ way up the stem. This continuum would make it necessary to set arbitrary limits to define the typical and woolly varieties. Therefore, the morphotype has not been recognized at any nomenclatural rank. These woolly plants could be mistaken for *C. floridana*, ignoring the inflorescence characteristics. They occur scattered through the range of the species.

The species inhabits open sandy soils, often disturbed, throughout much of the Florida peninsula. Its range extends to Miami on the east coast but it is absent from the Everglades-Lake Ochee-chobee region. A putative *Chrysopsis scabrella* \times *linearifolia* collection was made in Bradenton (Simpson s.n., F) with the odd flowering time of June. The plant has a mixture of traits between the two parents. At a site with *C. floridana* and *C. scabrella* fruit collected from the former species yielded plants of *C. floridana* and *C. floridana* \times *scabrella*, when grown at the University of Waterloo. The hybrid did not survive to maturity but did begin developing a corymbose inflorescence and had woolly stem leaves. The plant may have died because of unfavorable greenhouse conditions rather than due to innate genetic factors.

The species blooms from August to December and rarely in the Spring. The peak flowering period is September through October.

REPRESENTATIVE SPECIMENS. **Florida.** ALACHUA CO., W of Archer, *Small et al.* 10,043 (GH, NY, US); BREVARD CO., Indian River region, *Fredhom* 5,583 (GH, MO); BROWARD CO., Ft. Lauderdale, *Small & Carter* 1,036 (NY); CITRUS CO., Hwy 98, close to Hernando Co. line, *Lakela* 24,780 & 27,701 (USF); DIXIE CO., 13.5 mi S of Old Town, *R. K. Godfrey* 56,191 (GH, NY, FSU), E of Old Town, Suwannee River, *R. K. Godfrey* 75,780 (FSU, MO, WAT); FLAGLER CO., N of Bunnell, *Godfrey* 50,900 (FSU, NY); HERNANDO CO., Brooksville, *Jones* s.n. (US), 4 mi N of Brooksville, Chinesequit Wildlife Refuge, *Ray* 9,507 (USF); HIGHLANDS CO., E of Sebring, *Small & DeWinkeler* 9,786 (GH, NY, US); HILLSBOROUGH CO., Tampa, *Garber* s.n. (GH, MO, PH), Temple Terrace, *Godfrey* 59,166 (FSU); LEVY CO., between Janney and Vista, *Godfrey et al.* 64,787 (FSU); MANATEE CO., Manatee, *Simpson* s.n. (US); MARION CO., 3 mi S of Citra, *Murrill* s.n. (MO), W of Lake George, *Small* 8,962 (NY); MARTIN CO., Picture City, *Blake* 12,100 (GH); MONROE CO., N of Key Largo, *Jennings* 12,786 (USF); OSCEOLA CO., 5 mi NW of Loughman, *Ray et al.* 10,434 (GH, USF); PASCO CO., Jassamine, *Barnhart* 2,609 (NY); PINELLAS CO., Clear Water Harbor, *Chapman* s.n. (US); PUTNAM CO., 9 mi S of Melrose, *Godfrey* 69,166 (FSU), San Mateo, *Butts* s.n. (GH), W of Palatka,

Godfrey & Morrill 52,630 (FSU, GH); ST. LUCIE CO., W of the Sabastian River, *Small & DeWinkeler 9,730* (NY); TAYLOR CO., S of Perry, *Godfrey 60,397* (FSU, GH); VOLUSIA CO., Orange City, *Hood s.n.* (MO).

4. ***Chrysopsis floridana*** Small, Fl. SE U.S., 1339. 1903. TYPE: Florida, Braidenton, 28 November 1901. *Tracy 7,344* (HOLOTYPE, NY!; ISOTYPES, CU, F!, GH!, MINN, MO!, US!).

Chrysopsis mariana (L.) Ell. var. *floridana* (Small) Fern., *Rhodora* **39**: 455. 1937.

Heterotheca mariana (L.) Shinnars subsp. *floridana* (Small) Harms, *Wrightia* **4**: 13. 1968.

Heterotheca floridana (Small) Long, *Rhodora* **72**: 44. 1970.

Plants perennial, suffrutescent, the bases of old shoots giving rise to new growth, additional basal rosettes produced at the ends of short lateral rhizomes or roots. *Stems* erect or ascending, 3–7 dm tall, sometimes branching, densely short-woolly pubescent. *Basal rosette leaves* spatulate to oblanceolate, entire or apically dentate, 4–10 cm long, 1.5–2.5 cm wide, densely short-woolly, the hairs flagelliform. *Stem leaves* gradually reduced upward or hardly reduced to just below the capitulescence, obovate-elliptic, slightly auriculate-clasping, entire, sometimes undulate, mucronulate, densely short-woolly pubescent. *Capitulescence* subumbellate-cymose to more paniculate-cymose in branching shoots, 1–25 or more heads, lower branches sometimes flowering also; *peduncles* densely stipitate-glandular, 1–4 cm long with 0–4 linear glandular bracteoles. *Involucres* 5–8 mm high, campanulate; *phyllaries* in 3–4 unequal series, erect, linear, stipitate-glandular, 1 mm wide. *Ray florets* 15–20, strap 6–7 mm long, 1–2 mm wide. *Disc florets* 6–7 mm long, lobes 0.5 mm long. *Cypselas* straw colored, densely strigose, 2–2.5 mm long, smooth or faintly ribbed; *pappus* double, outer bristles short, inner bristles 5–6 mm long. *Chromosome number*: $n = 5$.

The morphology and distribution of *C. floridana* are illustrated in Figs. 4G and 9C–F. The species is easily recognised by its shrubby habit, short-woolly ovate to obovate stem leaves, and its subumbellate capitulescence. The species is very rare and found only on sandhills with Sand Pine in the Tampa Bay region. Only a half dozen populations are known, some of these very marginal for survival. The species will undoubtedly be placed on the rare and endangered species list for Florida and for the United States, a status it deserves. In full bloom it is the most striking of the species

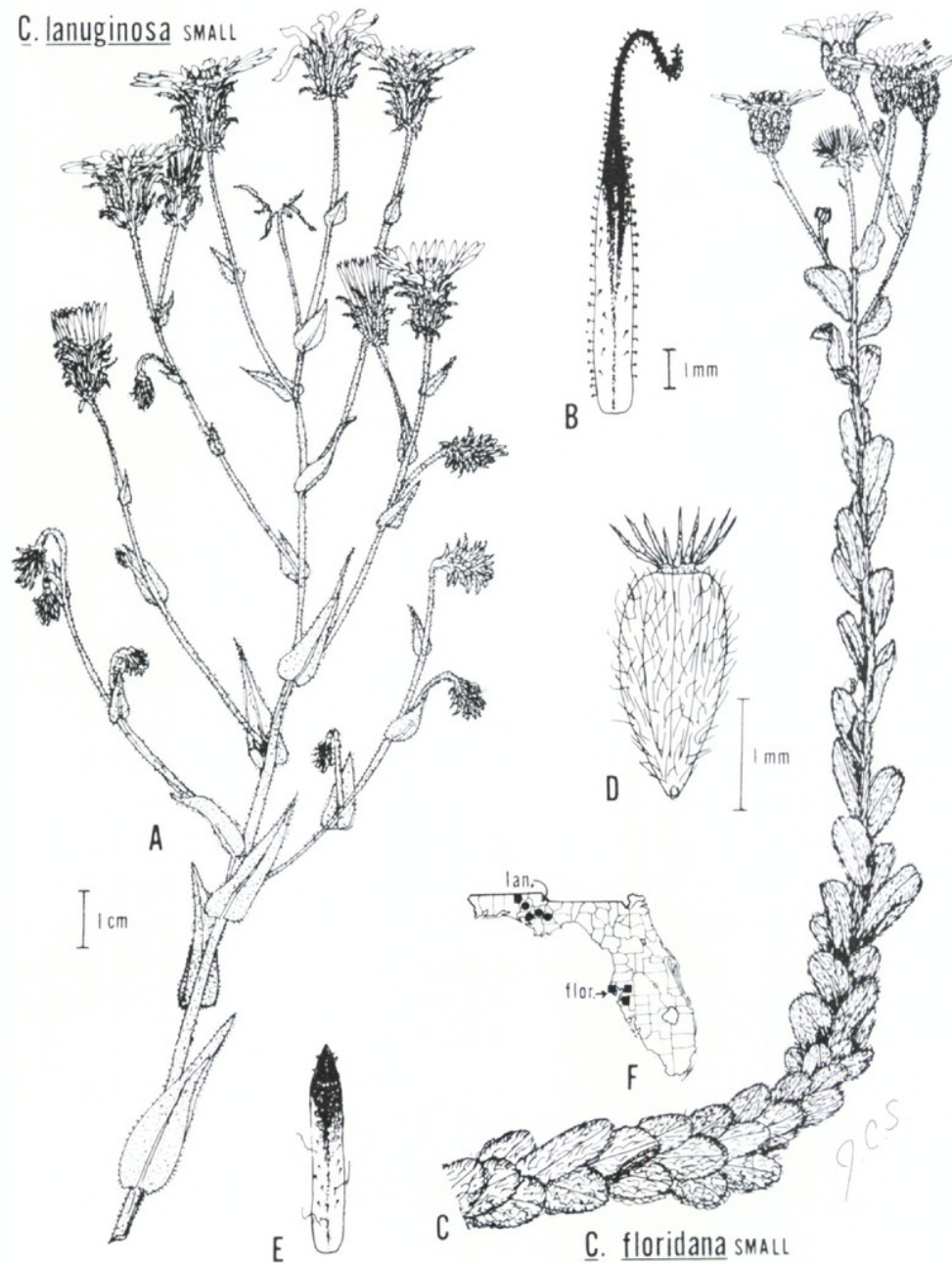


Figure 9. The morphologies and distribution of *C. lanuginosa* and *C. floridana*. A. & B. *C. lanuginosa*. A. Upper portion of stem with small capitulescence; robust plants may have up to 80 or more heads which nod in bud. B. Mid series phyllary. C.-E. *C. floridana*. C. Flowering shoot with a few-headed capitulescence; robust shoots may branch and have up to several dozen heads in a more paniculate arrangement; scale same as A. D. Disc floret cypsela; inner pappus bristles not illustrated. E. Mid series phyllary; same scale as B. F. County dot map of the distribution of *C. lanuginosa* (lan.) and *C. floridana* (flor.) based on all collections seen.

of this group of goldenasters. Its peak blooming period is December.

SPECIMENS EXAMINED. **Florida.** HILLSBOROUGH CO., scrub near Riverview, *Small s.n.* (NY), 5 mi E of Riverview, *Semple & Wunderlin 2,514* (MO, WAT), *Wunderlin 5,658* (MO, WAT, USF), S of Little Manatee River, Rustin, *Lakela 24,826* (FSU, USF) & *24,868* (USF), 0.7 mi S of Little Manatee River, Hwy. 11, *Semple & Wunderlin 2,502* (WAT); MANATEE CO.; between Braidenton and Braidenton Beach, *Godfrey 65,184* (FSU), Manatee, *Simpson s.n.* (US); PINELLAS CO., Long Key, dunes, *Small et al. 10,098* (NY, US).

5. ***Chrysopsis lanuginosa*** Small, Man. SE Fl. 1339. 1933. TYPE: Florida, near Lynn Haven, grassy places, *Van Cleve 11* (HOLOTYPE, NY!, aberrant specimen; ISOTYPE, US!).

Plants biennial, usually only one shoot arising from the basal rosette. *Stems* erect, 4–10 dm tall, densely stipitate-glandular, usually unbranched in the lower 2/3's. *Basal rosette leaves* oblanceolate, 3–8 cm long, densely long-woolly pubescent, the hairs flagelliform. *Stem leaves* sessile, clasping, linear-lanceolate to lanceolate, reduced upward, entire, densely stipitate-glandular on both surfaces. *Capitulescence* paniculate-cymose, (18–)30–80 heads nodding in bud; *peduncles* densely stipitate-glandular, 2–12 cm long, with 0–6 clasping glandular bracteoles. *Involucres* campanulate, 8–12 mm high; *phyllaries* in 3–4 unequal series, linear, the tips long-subulate, often twisted and reflexed, densely stipitate-glandular, 1 mm wide. *Ray florets* 12–31, averaging 19 per head, straps 8–11 mm long, 1.5–2.5 mm wide. *Disc florets* 5–6 mm long, lobes 0.5 mm long. *Cypselas* densely strigose, 2–2.5 mm long, straw colored; *pappus* double, the outer bristles short, the inner bristles 5–6 mm long. *Chromosome number*: $n = 5$.

The morphology and distribution of *Chrysopsis lanuginosa* are illustrated in Figs. 9A, B, and F. The species has a yellowish-green color in the field accented by the sometimes black-tipped glands. Small plants can be morphologically similar to robust individuals of *C. godfreyi* f. *viridis*, but are distinguished by their more paniculate capitulescence, their usually longer and more linear stem leaves and the linear, subulate phyllaries.

The species is endemic to a small region of western Florida to the north and east of the type locality in Bay County, Florida. The

species has apparently very recently expanded its range by colonizing greatly disturbed Slash Pine plantations after clear-cut logging operations (R. K. Godfrey, pers. comm.). Populations persist at such sites for a few years before other species colonize and cover the barren sandy soil. The numbers of individuals at such sites can reach into the thousands. In Calhoun County a population was found which included very robust plants that had flowering branches arising from nodes along the entire stem. Hundreds of heads were in bloom at the same time on these plants. The species blooms from October to December and rarely in the Spring.

REPRESENTATIVE SPECIMENS. **Florida.** BAY CO., Lynn Haven, *Godfrey 59,119* (FSU), N of Lynn Haven, jct. of Fla. 77 and Rte 20, *Godfrey 75,774a* (FSU, MO, USF, WAT), approx. 7 mi N of Panama City, *Godfrey & Houk 61,555* (FSU), 10.5 m N of Southport, *Godfrey 61,639* (FSU); CALHOUN CO., 6 mi W of Clarksville, *Godfrey & Semple 76,120* (FSU); HOLMES CO., 5.5 mi E of Argyle, *Godfrey & Semple 76,210* (FSU); LIBERTY CO., 4.5 mi E of Bristol, *Godfrey 75,712* (FSU, WAT, MO), between Hosford and Quincy, 0.8 mi from county line, *Godfrey 76,070* (FSU), Torreya State Park, *Godfrey 72,274* (FSU), White Springs E of Bristol, *Godfrey 64,667* (FSU); WASHINGTON CO., S of Chipley, Crystal Lake, *Godfrey 61,637* (FSU), 3 mi S of Wausau, *Godfrey 73,939* (FSU).

6. *Chrysopsis godfreyi* Semple, Can. J. Bot. **56**: 2092. 1978.

TYPE: Florida, Okaloosa Co.; US 98 E of Destin, dunes N of Silver Beach Wayside Park, 5 November 1977, *Semple & Godfrey 3,148* (HOLOTYPE, WAT!; ISOTYPES, FSU!, GH!, MO!, NY!, US!, USF!).

Plants biennial or perennating by means of basal rosettes developing along the previous season's growth at soil level. *Stems* solitary and unbranched to branched in robust plants, decumbent or ascending to erect, 2–5 dm tall, woolly basally and either woolly apically or densely stipitate-glandular. *Basal rosette leaves* oblanceolate, obtuse, sparsely dentate-serrate apically, to 10 cm long, long-woolly on both surfaces, hairs flagelliform. *Stem leaves* ovate to linear-lanceolate, entire, sometimes strongly clasping, woolly or glabrous and densely stipitate-glandular, acute, either abruptly or gradually reduced below the inflorescence. *Capitulescence* corymbose-cymose to corymbose-paniculate in robust plants, 5–15 (25) heads nodding in bud; *peduncles* densely stipitate-glandular, bracteoles either glabrous-glandular or densely woolly. *Involucres* campanulate, 9–12 mm high; *phyllaries* 4–5 unequal series, attenuate

to subulate, tips spreading to recurved, densely stipitate-glandular. *Ray florets* 16–36, averaging 25 per head, straps 10–15 mm long. *Disc florets* 6–7 mm long, lobes 0.5–1 mm long. *Cypselas* straw colored 2–2.5 mm long, densely strigose, shallowly ribbed; *pappus* double, outer bristles short, inner bristles 6–7 mm long. *Chromosome number*: $n = 5$.

C. godfreyi SEMPLE

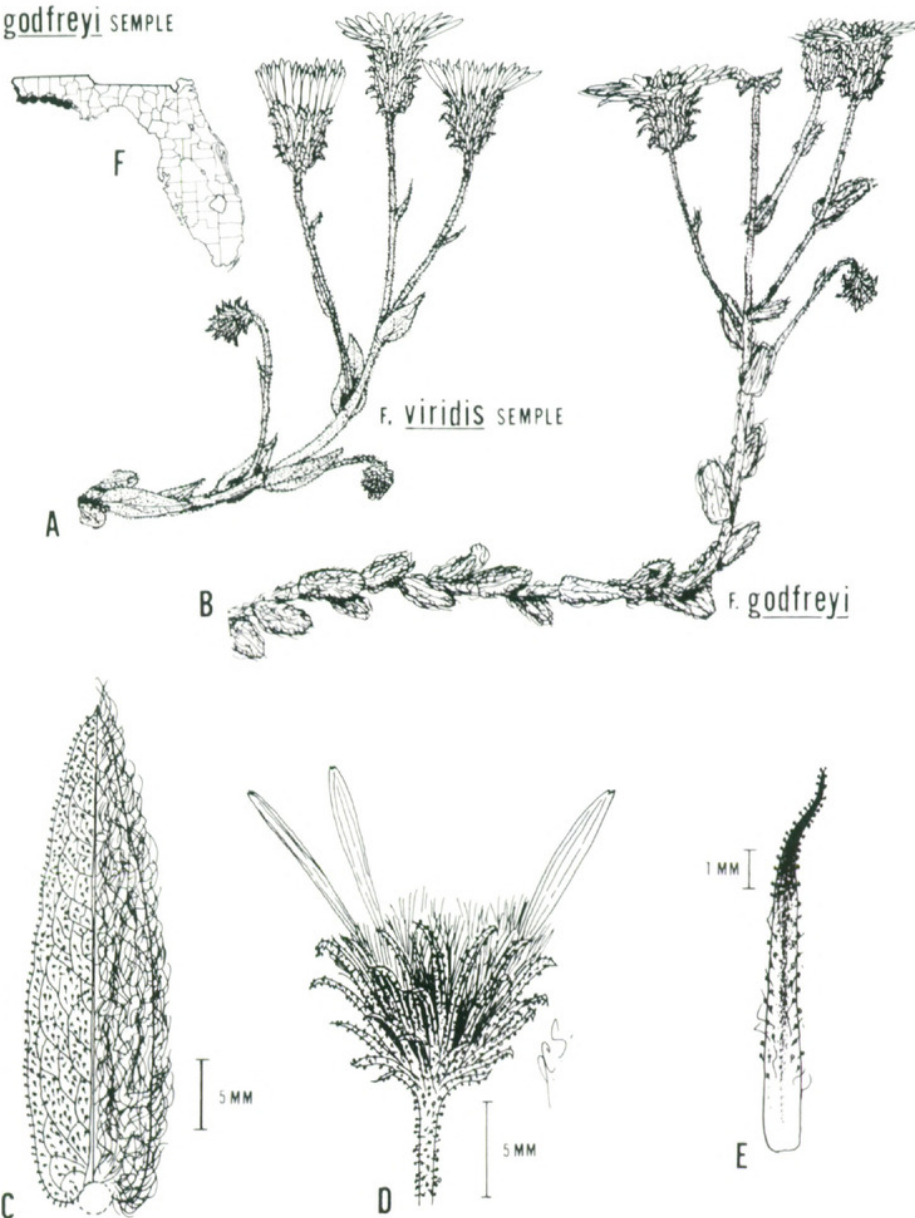


Figure 10. The morphology and distribution of *C. godfreyi*. A. Stem of *f. viridis*. B. Stem of *f. godfreyi*. C. Mid stem leaf; left side drawn as *f. viridis*, right side drawn as *f. godfreyi*. D. Head of either form. E. Mid series phyllary. F. County dot map of the distribution based on herbarium collections and field observations.

The morphology and distribution of *Chrysopsis godfreyi* are illustrated in Figs. 4A and F and 10A–F. The habit varies from nearly procumbent to fully erect depending upon the habitat and the age of the plant. The shape of the phyllaries varies from west to east, the least subulate occurring in the east in Bay County. The merely attenuate phyllaries and few-headed cymose capitulescence distinguish the eastern plants of f. *viridis* from *C. lanuginosa* to which it is closely related. Two forms occurred at all locations visited.

The species is endemic to the Gulf coast barrier islands of western Florida. The eastern limits are reached in Bay County, the western near Alabama. The species grows in deep sand, often serving to stabilize dunes. It can occur in small populations of a few individuals or in very large populations of hundreds of plants in relatively open natural dunes or open cleared lots.

6a. *Chrysopsis godfreyi* f. *godfreyi*.

This form is distinguished from the next by its densely long-woolly pubescence on the stem leaves and peduncular bracts.

REPRESENTATIVE SPECIMENS: (see Semple, 1978a).

- 6b. *Chrysopsis godfreyi* f. *viridis* Semple, Can. J. Bot. **56**: 2093. 1978. TYPE: Florida, Okaloosa Co.; US 98 E of Destin, dunes N of Silver Beach, Wayside Park, 5 November 1977, Semple & Godfrey 3,139 (HOLOTYPE, WAT!; ISOTYPES, FSU!, GH!, MO!, NY!, US!, USF!).

This form is distinguished by its green, densely stipitate-glandular stem leaves and peduncle bracts.

REPRESENTATIVE SPECIMENS: (see Semple, 1978a).

7. *Chrysopsis latisquamea* Pollard, Proc. Biol. Soc. Wash. **13**: 131. 1900. TYPE: Florida, Clarona, *M. Meislahn 15a* (HOLOTYPE US!, ISOTYPE NY!).

Heterotheca latisquamea (Pollard) Harms, Castanea **39**: 163. 1974.

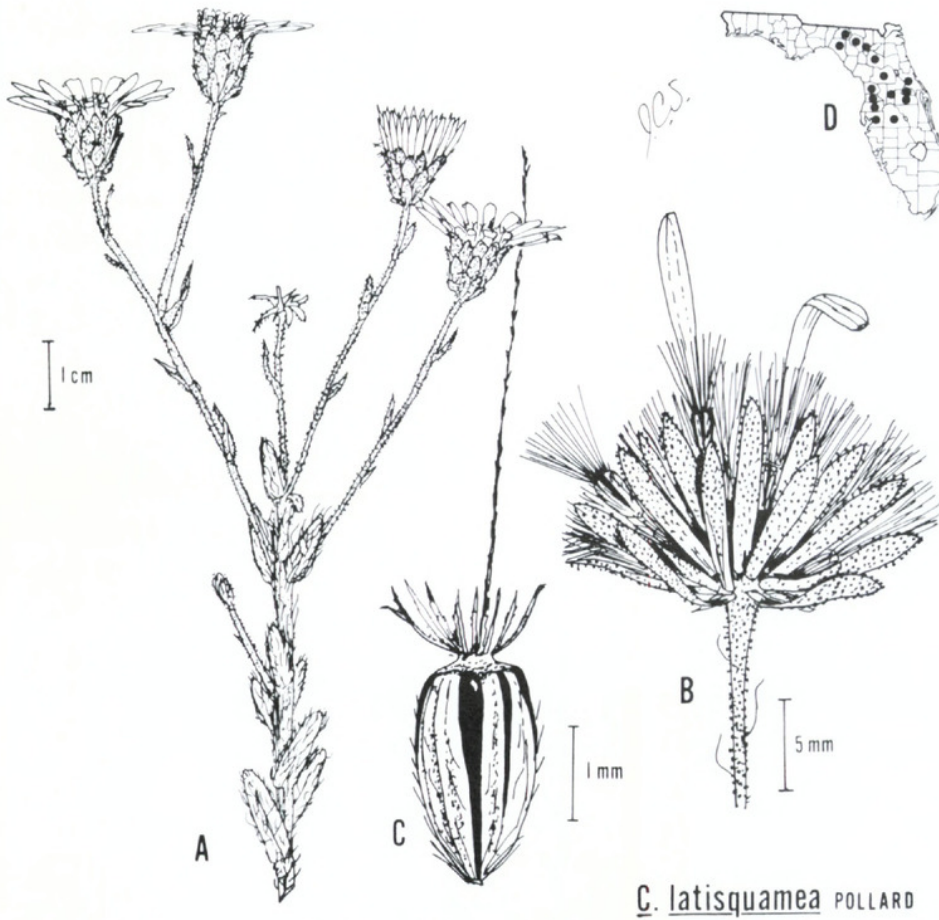
Plants biennial or weakly perennial, usually one shoot arising from the basal rosette. *Stems* unbranched to branching from below the middle, 4–7 dm tall, erect, long-woolly pubescent below, becoming densely stipitate-glandular above. *Basal rosette leaves*

oblanceolate, obtuse, to 8 cm long and 2 cm wide, densely long-woolly, the hairs flagelliform. *Stem leaves* reduced upward, sessile, elliptic to ovate, entire, obtuse, mucronulate, densely long-woolly, the upper-most leaves less so and stipitate-glandular. *Capitulescence* lax to compact corymbose-cymose, individual branches with 1–5 heads, to 60 heads per plant; *peduncles* densely stipitate-glandular, 1–6 (10) cm long, bracteoles stipitate-glandular, ovate to lanceolate. *Involucres* campanulate, 8–11 mm high; *phyllaries* in 2–3 unequal series, 1.5–2.5 mm broad, stipitate-glandular, oblanceolate, acute. *Ray florets* 10–18 averaging about 14 per head, straps 10–15 mm long, 2–3.5 mm wide. *Disc florets* 6.5–8.5 mm long, lobes 1 mm long. *Cypselas* sparsely strigose, ribbed, 1–3 narrow to broadly clavate, yellow to red-brown translucent ridges per side, 2–3 mm long; *pappus* double, outer bristles short, inner bristles 7–9 mm long. *Chromosome number*: $n = 5$.

The morphology and distribution of *Chrysopsis latisquamea* are illustrated in Figs. 4A and B and 11A–D. The species is distinctive and easily recognised by its light green involucres with broad foliaceous, stipitate-glandular phyllaries, its long-woolly pubescent leaves, and the translucent ridges on the fruits. It occurs sympatrically with *C. gossypina* in the northwestern part of its range; it has been confused with broad-phyllaried forms of the latter. The heads of the *C. gossypina* subsp. *gossypina* in the region of sympatry are never densely stipitate-glandular and have a darker green color, not yellow-tinged. The habit varies from a single erect unbranched stem to ramose, spreading forms. The latter forms also could be confused with forms of *C. gossypina* which can manifest this habit. No evidence of hybridization was found at several populations visited in 1976. One of these sites was a disturbed lot with dozens of individuals of both taxa intermixed and blooming at the same time. No herbarium collections appear to be hybrids either.

The species grows throughout most of northeastern Florida as far south as Tampa. It grows in sandy, open soils of pine woods and scruboak communities and in disturbed soils along road embankments and cleared lots. It blooms from August to October and occasionally as early as May.

REPRESENTATIVE SPECIMENS. **Florida.** ALACHUA CO., Waldo, *Gilman s.n.* (MO); CITRUS CO., Hernando, *Degener 5,237* (NY), 4 mi NW, *Kral 6,891* (USF); COLUMBIA CO., Lake City, *Hitchcock 900* (F), S of town, *Godfrey 50,829* (NY); HERNANDO CO., Brooksville,



C. latisquamea POLLARD

Figure 11. The morphology and distribution of *C. latisquamea*. A. Flowering stem with a few-headed inflorescence; the number of heads can be much greater. B. Dried head with only a few ray florets drawn. C. Disc floret fruit with only one of 30–35 long pappus bristles drawn. D. County dot map of the distribution based on all collections seen.

4.5 mi N, *Godfrey* 50,859 (FSU), Choocochattee Hammock, *Small et al.* 10,603 (NY), 6 mi N at Chinesequit Hill, *Cooley* 6,900 (USF), *Ray* 9,393 (USF); HILLSBOROUGH CO., 12 mi N of Tampa, *Blanton* 6,644 (F, GH, USF), Tampa, *Garber* s.n. (F, GH, NY, PH, US); LAKE CO., Eustis, *Hitchcock* 899 (F, MO), *Nash* 970 (PH), *Nash* 1,307 (GH, MO, NY, US); MADISON CO., E of Madison *Godfrey* 53,960 (USF), *Norris* 638 (USF); MARION CO., 3 mi N of Ocala, *Blanton* 6,636 (GH, MO); ORANGE CO., Beresford, *Hood* s.n. (MO), Lake Brantley, *Lewton* s.n. (PH), 1 mi E of Orlando, *O'Neill* 5,596 (US); SEMINOLE CO., Forest City, *Lewton* s.n. (NY); VOLUSIA CO., Lake Helen, *Webster* s.n. (US).

8. *Chrysopsis linearifolia* Semple, *Brittonia* 30:493. 1978. TYPE: Florida. Franklin Co.; US 98 just S of the Ochlockonee River, open sandy ridge, adjacent to longleaf pine-scrub-[oak] road stand, 2 November 1976, *Godfrey* 75,745 (*Holotype*, MO!, *Isotypes*, FSU!, GH!, NY!, USF!, WAT!).

This species is equivalent to *C. hyssopifolia* of nearly all previous authors, who misapplied the name. Semple (1978b) noted the reasons for this incorrect nomenclature.

Plants biennial, rarely perennating by production of basal rosettes. *Stems* erect and unbranched usually, 3–20 dm tall, glabrous, often reddish-purple. *Basal rosette leaves* to 10 cm long, oblanceolate to linear-oblanceolate, glabrous to densely woolly, the hairs flagelliform. *Stem leaves* entire, linear to linear-lanceolate, glabrous, margins occasionally undulate, acute to obtuse. *Capitulescence* subumbellate or loosely open corymbose-cymose (4) 20–100 heads; *peduncles* glabrous. *Involucres* campanulate, 6–10 (12) mm high; *phyllaries* in 4–5 unequal series, glabrous, a few stipitate-glands at the bases of the outer series, acute, appressed. *Ray florets* 10–30, straps 9–12 mm long. *Disc florets* 5–6 mm long, lobes 0.5–1 mm long. *Cypselas* sparsely strigose, straw colored, 2–2.5 mm long, weakly ribbed and with 1–3 golden-yellow to red-brown clavate, translucent ridges per side; *pappus* double, outer bristles short, inner bristles 4–6 mm long. *Chromosome number*: $n = 5$.

The morphology and distribution of *C. linearifolia* are illustrated in Figs. 4B, C and D and 12A–G. Two subspecies are recognised. Both subspecies occur in sandy soils of pine and oak woods and scrublands and in disturbed open soils such as are found along roadsides and in cleared lots. The species blooms from September through November and in the Spring on occasion, particularly in southern Florida.

8. *Chrysopsis linearifolia* subsp. *linearifolia*.

The panhandle Florida taxon is distinguished by its compact subumbellate-paniculate capitulescence of (10) 30–100 heads with 10–20 rays and its very narrow stem leaves. The basal rosettes often have a mixture of woolly and glabrous leaves, the difference appearing to be due to the time of development. Depaupered plants of this subspecies could be confused with linear-leaved forms of *C. gossypina* subsp. *hyssopifolia*, which differ in having ciliate leaf margins and a chromosome number of $2n = 18$.

REPRESENTATIVE SPECIMENS: (see Semple, 1978b).

8b. *Chrysopsis linearifolia* subsp. *dressii* Semple, Brittonia 30: 493–494, 1978. TYPE: Florida; Brevard Co., Merritt Is.,

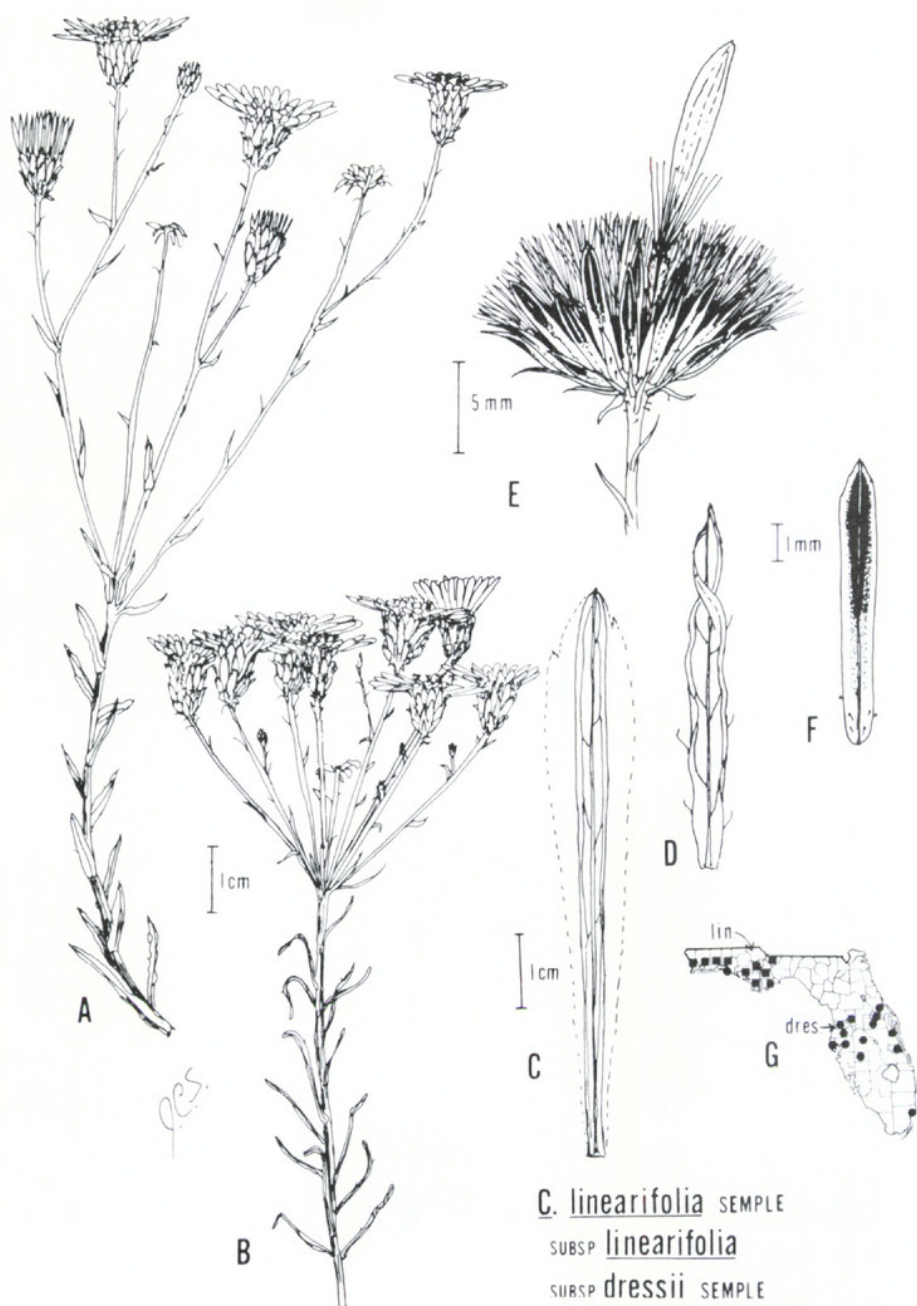


Figure 12. The morphology and distribution of *C. linearifolia*. A. Blooming shoot of subsp. *dressii*. B. Small blooming shoot of subsp. *linearifolia*; these shoots can be up to 2m tall with up to 100 heads. C. Basal rosette leaf; the broken line indicates an alternative form which can be densely woolly pubescent, as can the linear form; the upper stem leaves of subsp. *linearifolia* are similar to the glabrous linear form. D. Undulate stem leaf of subsp. *dressii*; scale same as C. E. Dried head with only one ray floret drawn. F. Mid series phyllary. G. County dot map of the distribution of the two subspecies (subsp. *linearifolia*- "lin"-squares; subsp. *dressii*- "dress"-dots) based on all collections seen.

Dummit Cover, Rte. 3, 2 Oct. 1976. *Semple, Wunderlin, Poppleton & Norman 2530* (HOLOTYPE, MO!; ISOTYPES, US!, USF!, WAT!).

This primarily peninsular Florida taxon is distinguished by its loosely corymbose-cymose capitulescence of 4–30 (50) heads with 20–30 ray florets and its often undulate-margined, narrow, lanceolate-elliptic stem leaves. The plants of the peninsula could be confused with very sparsely pubescent forms of *Chrysopsis subulata*, differing in their twisted, subulate phyllaries. The rare individuals of this subspecies found near the coast of western Florida are similar to forms of *C. gossypina* subsp. *cruiseana*, which differ in having a compact subumbellate capitulescence and a chromosome number of $2n = 18$.

REPRESENTATIVE SPECIMENS: (see Semple, 1978b).

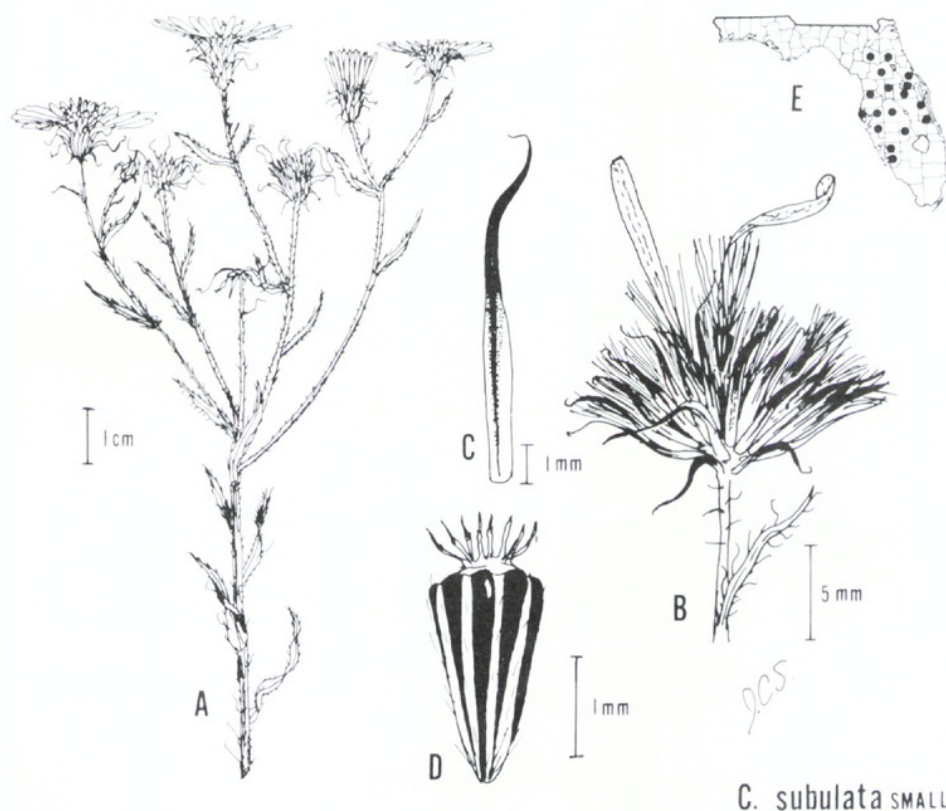
9. ***Chrysopsis subulata*** Small, Man. SE Fl. 1338. 1933. TYPE: Florida, scrub between Avon Park and Sebring, 17 July 1924, *Small, Small & DeWinkler 11,495* (Holotype, NY!, Isotypes, GH!, US!).

Heterotheca hyssopifolia (Nutt.) Long var. *subulata* (Small) Long, *Rhodora* **72**: 43. 1970.

Plants biennial, frequently perennating by means of basal rosettes produced at the bases of old stems and at the ends of short lateral rhizomes and roots. *Stems* often much branched near the base, sometimes through damage, 2–7 dm tall, sparsely pubescent, sometimes purple-tinged. *Basal rosette leaves* oblanceolate to linear-oblanceolate, first season leaves densely long-woolly, the hairs flagelliform, other seasons sparsely to densely long-woolly, 5–10 cm long. *Stem leaves* linear-lanceolate, entire, often undulate margined, acute, marginally ciliate, reduced upward and becoming linear, sparsely pubescent. *Capitulescence* lax cymose, a few heads per branch; *peduncles* thin, 1–10 cm long, glabrous-glabrate, bracteoles ciliate margined. *Involucres* campanulate, 8–10 mm high; *phyllaries* in 4–5 unequal series, linear, long subulate (very rarely acute), the tips twisted and reflexed to spreading, glabrous or with a few stipitate glands at the bases. *Ray florets* 10–28, averaging about 18 per head, straps 5–8 (–10) mm long, 1.5–2 mm wide. *Disc florets* 5–6

mm long, lobes 0.5 mm long. *Cypselas* narrowly compressed-obconic, 1.5–2 mm long with several to many yellow to dark red-brown, clavate, translucent ridges; *pappus* double, outer bristles short, inner bristles 6–7 mm long. *Chromosome number*: $n = 5$.

The morphology and distribution of *Chrysopsis subulata* are illustrated in Figs. 13A–E. The species is easily identified by its long subulate phyllaries typical of all populations but a few in Alachua County, Florida. These plants have a normal habit and leaf character, but the phyllaries are merely acute like those of *C. linearifolia*, with which it could be confused for this reason. Such plants could also be confused with *C. gossypina* f. *trichophylla*, with which there has been some nomenclatural confusion as well. The fruits vary in the number of ridges and the size. At one extreme they are similar to those of other species (Fig. 11C). At the other end they are noticeably smaller, narrower, and have many ridges which



C. subulata SMALL

Figure 13. The morphology and distribution of *C. subulata*. A. Flowering branch, upper portion. B. Dried head with only a few ray florets drawn. C. Mid series phyllary. D. The extreme form of disc fruit with narrow body and many translucent ridges; the other extreme is like that shown in Fig. 11C. E. County dot map of the distribution based on all collections seen.

nearly cover the entire surface of the fruit (Fig. 13D). The habit also varies from fairly unbranched to much branched from near the bases or along much of the stem. The plants readily perennate by means of basal rosettes produced at the ends of short lateral rhizomes or roots. Small clones can form in this way.

The species grows in a broad central zone of the Florida peninsula. It inhabits open sandy soils of pine woods and oak scrublands and open disturbed soils of roadsides and cleared lots. Its peak blooming period is earlier than the other species native to Florida. It flowers from May to September, peaking in July and August. Dr. R. P. Wunderlin (pers. comm.) has noted that these early blooming shoots often have a second flush of blooming in mid to late Fall. Thus, plants can be found from October to December with flowering heads, but otherwise brown and dried stems, the leaves having dropped off for the most part.

REPRESENTATIVE SPECIMENS. **Florida.** ALACHUA CO., Gainesville, N of Lake Warburg, *Murrill* 229 (MO, US); BREVARD CO., Eau Gallie, *Curtiss* 1,364 (NY, US), Melbourne, *Curtiss* 5,733 (GH, NY, US), N Merritt Is. *Shuey & Poppleton* s.n. (USF); CHARLOTTE CO., Salt Springs, Myakka Peninsula, *Small et al.* 10,609 (NY); FLAGLER CO., N of Ormond, *Butts* s.n. (GH); HERNANDO CO., *Hitchcock* 898 (MO), Brooksville area, *Jones* 29 (US), Choochochattee Hammock, *Small et al.* 11,477 (NY), sand hills, *Mosura* s.n. (USF); HILLSBOROUGH CO., Ruskin, *Blanton* 6,753 (F), Sutherland, *Barnhart* 2,741 (NY), Tampa, *Lakela* 32,053 (USF), *Britton & Wilson* 17 (NY), U.S.F. campus, *Lakela* 24,158 (USF); INDIAN RIVER CO., near Felsmere, *Small* 8,901 (GH, NY, US); LAKE CO., near Eustis, *Nash* 1,239 (GH, NY, US), *Nash* 1,575 (PH); MANATEE CO., Braidenton, *Tracy* 7,073 (GH, NY, US), *Genelle & Fleming* 2,071 (USF), S of Duette, *Shuey* 1,651 (USF); MARION CO., 5 mi W of Asor Park, *Kral* 7,672 (USF); ORANGE CO., pine barrens, *Fredholm* 5,356 (GH, NY), Bithlo, *O'Neil* s.n. (US), Clarcona, *Meislahn* 144b (US), E of Orlando, *Lakela* 24,380 (USF); PINELLAS CO., E of Clearwater, *Kral* 7,460 (USF), St. Petersburg, *Williams* s.n. (PH); POLK CO., Crooked Lake area, *Lakela* 24,193 (USF); PUTNAM CO.; 2 mi S of Crescent City, *Butts* s.n. (GH). SEMINOLE CO., Banford, *Betting* 317 (F); VOLUSIA CO., *Poppleton* 891 (USF), Ormond, *Purdie* s.n. (GH), Pierson, *Dowell* 7,590 (NY).

10. ***Chrysopsis gossypina* (Michx.) Ell.** Sketch Bot. S.C. and Ga. 2: 337. 1824. TYPE: Lieux arides en Basse Caroline, fleurit en Septembre, *Michaux* s.n. (P, seen on microfiche only).

?*Erigeron pilosum* Walt., Fl. Car. 206. 1788, nom. nud.

Inula gossypina Michx. Fl. Bor. Am. 2: 122. 1803.

Diplopappus lanatus Cass., Dict. des Sc. Nat. 13:309. 1819.

Chrysopsis dentata Ell., Sketch Bot. S.C. and Ga. 2: 337. 1824.

Chrysopsis gossypina (Michx.) Ell. β *dentata* (Ell.) T. & G., Fl. North Amer. 2: 254. 1842.

Diplogon pilosa (Walt.) Kuntze, Rev. Gen. 334. 1891.

Chrysopsis pilosa (Walt.) Britt., Mem. Torr. Bot. Club 5: 316. 1894 (non Nutt. 1834).

Heterotheca gossypina (Michx.) Shinnars, Field & Lab. 19: 71. 1951.

Three subspecies are recognized in this highly variable allopolyploid complex. These are described below.

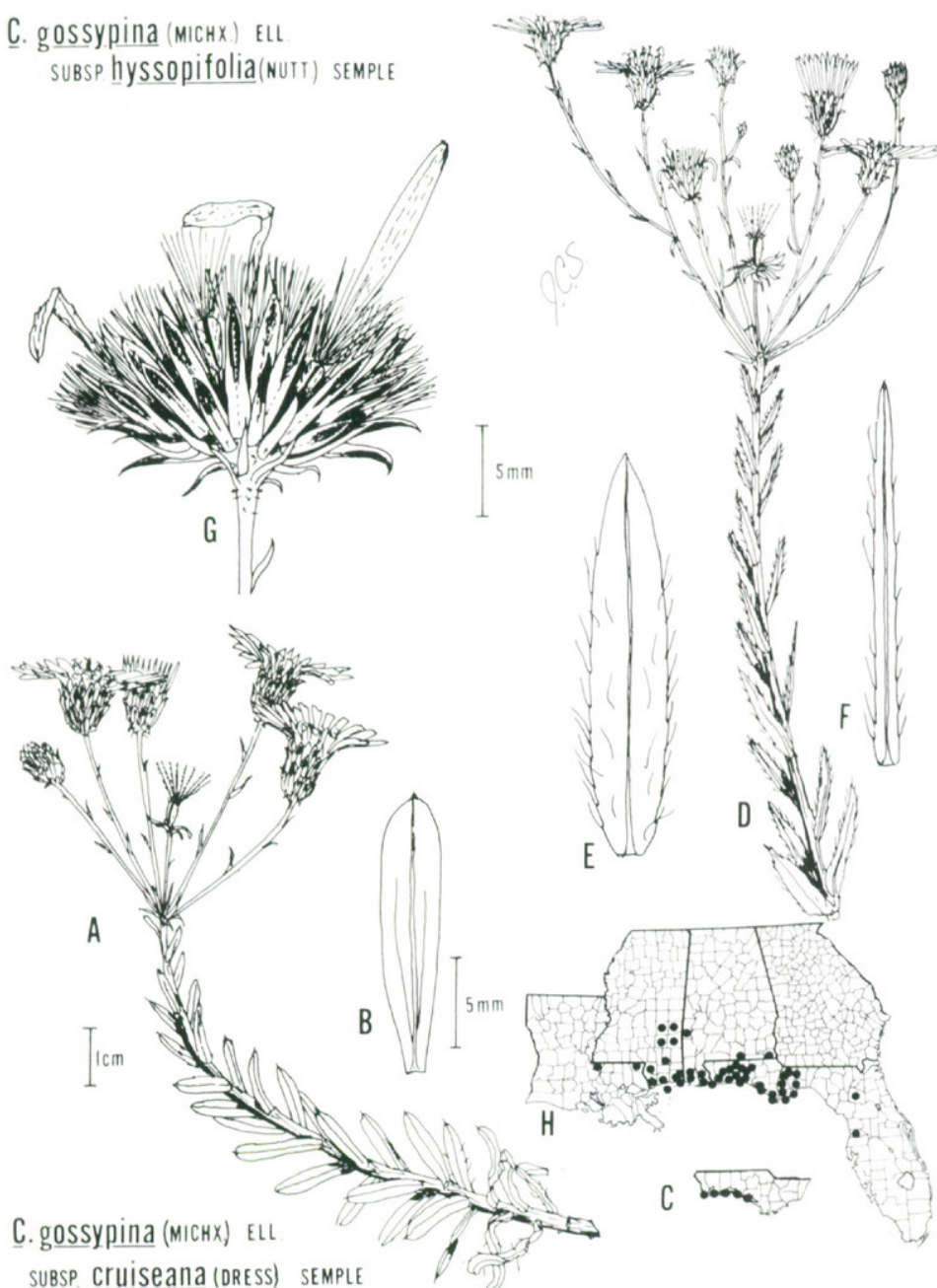
10a. ***Chrysopsis gossypina* subsp. *cruiseana*** (Dress) Semple, Can. J. Bot. 58: 147. 1980.

Chrysopsis cruiseana Dress, Gentes Herb. 8: 404–406. 1954. TYPE: Florida, Santa Rosa Island, about 2 mi E of Pensacola Beach, in white sand on level ground and on dunes well back from the outer beach, 27 December 1953, Dress & Cruise 2,822 (Holotype, BH); Santa Rosa Island, 28 May 1903, Tracy 8,539 (Paratypes, F!, GH!, MINN, MO!, US!).

Plants perennial, older ones developing up to 80 shoots from persistent bases of old stems. *Stems* usually decumbent, unbranched, 2–6 dm long, glabrous, often purple-tinged. *Basal rosette leaves*, 3–10 cm long, oblanceolate, densely long-woolly, the hairs flagelliform, apically dentate. *Stem leaves* elliptic to oblanceolate, 1–3 cm long, mucronulate, glabrous, acute to obtuse, entire, the lower ones dropping off stem by the time of flowering. *Capitulescence* subumbellate-cymose, (3) 10–30 heads; *peduncles* glabrous, 2–8 cm long, bracteoles oblanceolate, glabrous. *Involucre*s campanulate, 8–12 mm high; *phyllaries* in 4–5 unequal series, linear, 1–1.5 mm wide, acute, the tips appressed to slightly spreading, glabrous, a few stipitate glands at the bases of the outer ones. *Ray florets* 17–27, averaging about 23 per head, straps 7–10 (12) mm long, 2–3 wide. *Disc florets* 6–7 mm long, lobes 0.5 mm long. *Cypselas* sparsely strigose, 2.5–3 mm long, shallowly ribbed, 1–3 yellow to red-brown clavate, translucent ridges per side; *pappus* double, outer bristles short, inner bristles 6–8 mm long. *Chromosome number*: $n = 9$.

The morphology and distribution of *Chrysopsis gossypina* subsp. *cruiseana* are illustrated in Figs. 4H and 14A–C. The plants are perennial; the shoots of older plants are decumbent, while the first shoot may be erect. The number of shoots varies with age and growing conditions. As many as 80 shoots can be produced in a season by plants growing in sheltered dune habitats. Plants more exposed to sea air are often stunted.

C. gossypina (MICHX.) ELL.
SUBSP. *hyssopifolia* (NUTT.) SEMPLE



C. gossypina (MICHX.) ELL.
SUBSP. *cruiseana* (DRESS.) SEMPLE

Figure 14. The morphology and distribution of *C. gossypina* subsp. *cruiseana* and subsp. *hyssopifolia*. A.-C. subsp. *cruiseana*. A. Flowering shoot with a few heads. B. Mid stem leaf. C. County dot map of the distribution based on all collections seen. D.-H. subsp. *hyssopifolia*. D. Flowering shoot; scale same as A. E. & F. Stem leaves; scale same as B. G. Dried head; the heads of subsp. *cruiseana* and subsp. *gossypina* f. *trichophylla* are similar. H. County dot map of the distribution based on all collections seen.

The subspecies inhabits sandy dunes on the Gulf Coast barrier islands of Alabama and Florida. It blooms from October to December.

REPRESENTATIVE SPECIMENS. **Florida.** ESCAMBIA CO., Santa Rosa Is. Nat'l Seashore area, *Godfrey* 73,965 (FSU), 4 mi E of Pensacola Beach, *McDaniel* 7,179 (MO); OKALOOSA CO., E of Destin, *Godfrey* 73,954 (FSU), 2 mi E of Fort Walton, *McDaniel* 5,483 (FSU), E of Fort Walton Beach, *Godfrey* 76,165 (FSU); SANTA ROSA CO., 3 mi E of Pensacola Beach bridge, *Ward* 1,729 (GH), 17.5 mi E of Pensacola Beach, *McDaniel* 7,167 (FSU, MO), W of Gulf Is. Nat'l Seashore, *Boufford et al.* 18,584 (MO); WALTON CO., Seagrove Beach, *Godfrey* 75,771 (FSU, MO, WAT), E of Grayton Beach State Park, *Ward* s.n. (FSU, USF).

- 10b. *Chrysopsis gossypina* subsp. *hyssopifolia* (Nutt.) Semple, Can. J. Bot. **58**: 147. 1980. *Chrysopsis hyssopifolia* Nutt., J. Acad. Phila. **7**: 67. 1834. TYPE: W. Florida, *Ware* s.n. (Holotype, PH!).

Chrysopsis trichophylla (Nutt.) Ell. β *hyssopifolia* (Nutt.) T. & G., Fl. North Amer. **2**: 254. 1842.

Chrysopsis trichophylla (Nutt.) Ell. var. *hyssopifolia* (Nutt.) Chapman, Fl. S.U.S. 216. 1860.

Diplogon hyssopifolia (Nutt.) Kuntze, Rev. Gen. 334. 1891.

Chrysopsis gigantea Small, FL. S.E.U.S. 1939. 1903. TYPE: Florida, *Leavenworth* s.n. (HOLOTYPE, NY!; ISOTYPE, GH!).

Chrysopsis mixta Dress, Gentes Herb. **8**: 404-406. 1954. TYPE: Florida, 5.5 mi E of Argyle on US-90, 2 Oct. 1953. *Dress* 2,689 (HOLOTYPE, BH).

Heterotheca hyssopifolia (Nutt.) Long, Rhodora **72**: 42-43. 1970.

Heterotheca hyssopifolia (Nutt.) Harms, Castanea **39**: 163. 1974.

Plants perennial, sometimes biennial, propagating by basal rosettes produced at the lowest nodes of old stems and at the ends of short to long lateral rhizomes or roots. *Stems* erect or ascending, 2-7 dm tall, glabrous or sparsely pubescent, often purple-tinged, solitary or several from a common rosette. *Basal rosette leaves* oblanceolate, 3-10 cm long, apically dentate or entire, sparsely to densely long-woolly, the hairs flagelliform, perennating rosettes often sparsely woolly. *Stem leaves* linear to linear-lanceolate, sparsely pubescent to glabrous, the margins ciliate, reduced upward, ascending. *Capitulescence* subumbellate-cymose, sometimes corymbose-cymose, 1-15(25) heads; *peduncles* glabrate, 1-6 cm long, bracteoles linear to linear-lanceolate, often ciliate along the margins. *Involucres* 8-11 mm high, campanulate; *phyllaries* in 4-5

unequal series, linear, tips spreading to recurved, acute, glabrous. *Ray florets* 9–23, averaging 17 per head, straps 7–11 mm long, 1.5–2 mm wide. *Disc florets* 6–8 mm long, lobes 0.5–1 mm long. *Cypselas* sparsely strigose, 2.5–3 mm long, shallowly ribbed, 1–3 yellow to red-brown clavate, translucent ridges per side; *pappus* double, outer bristles short, inner bristles 5–7 mm long. *Chromosome number*: $n = 9$.

The morphology and distribution of *Chrysopsis gossypina* subsp. *hyssopifolia* are illustrated in Figs. 4I and 14D–H. Usually the plants develop one erect shoot with a compact subumbellate inflorescence of a few heads. Damaged plants in the central and western portion of the range are branched and the peduncles long and branched giving the plant an appearance like those occurring further east within the range of subsp. *gossypina*. Plants found in the central part of the range have the narrowest leaves and look the least like individuals of subsp. *gossypina*. Such linear-leaved plants could be confused with *C. linearifolia* subsp. *linearifolia*, which has a chromosome number of $2n = 10$ and lacks the ciliate leaf margins typical of *C. gossypina* subsp. *hyssopifolia*. The subspecies intergrades with the other two subspecies where ranges overlap. Some plants are assigned to a subspecies only with difficulty, since they have characteristics of both, or of all three. This is particularly true for plants from Bay, Gulf, Liberty, Franklin, Gadsden, Leon, and Wakulla Counties in Florida. In this region the plants are easily confused with subsp. *gossypina* f. *trichophylla*. At points where the mainland is in contact with the barrier island chain on the Gulf coast subspecies *hyssopifolia* hybridizes with subsp. *cruiseana*.

The subspecies grows in open sandy soils and disturbed sites in pine woods and oak scrub and by roadsides and cleared lots. Colonies are usually small under natural conditions, but can include dozens of plants, when disturbed sites are occupied.

The subspecies blooms from October to December.

REPRESENTATIVE SPECIMENS. **Alabama.** BALDWIN CO., Lillian, *Shinners* 28,908 (FSU), S of Seminole, *McDaniel* 3,918 (FSU); CHOCTAW CO., N of Toxey, *McDaniel* 9,826 (FSU); COVINGTON CO., E of Florala, *Kral* 33,651 (FSU); ESCAMBIA CO., Wilson, *Mohr* s.n. (US); HOUSTON CO., N of Crosby, *Godfrey* 67,508 (FSU); MOBILE CO., NE of Theodore, *Pennell* 4,491 (NY). **Florida.** ESCAMBIA CO., Pensacola, *Mohr* s.n. (US), near Bayou San Marcus Creek, *Kral & Godfrey* 6,033 (FSU); OKALOOSA CO., E of Crestview, *Godfrey* 76,197 (FSU), W of Ft. Walton Beach near county line, *Godfrey &*

Semple 76,173 (FSU), NE of Holt, *Godfrey* 59,028 (FSU), NW of Niceville, *Chapman* 194 (USF); SANTA ROSA CO., NW of Buxton, *Godfrey & Houk* 62,539 (FSU), E of Gulf Breeze, *McDaniel* 5,302 (FSU); WALTON CO., W of Portland, *Chapman & Smith*, 1,150 (USF), near Mossyhead, *Dress* 2,694 (FSU), E of Destin, *McDaniel* 5,460 (FSU). **Louisiana.** WEST FELICIANA PARISH, Jackson, *Drummond* 85 (GH); WASHINGTON PARISH, NW of Sheridan, *Ewan* 19,443 (FSU). **Mississippi.** HARRISON CO., Biloxi, *Tracy & Lloyd* 5,450 (GH, NY); JONES CO., W of Eastabuchie, *Jones* 10,282 (FSU); MOBILE CO., Dauphin Is., *Deramus* D-1023 (GH).

The following collections have the capitulescence and habit of subsp. *gossypina* and the ciliate leaf margins and often the leaf shape of subsp. *hyssopifolia*:

Florida. BAY CO., E of Tyndall, *McDaniel* 3,830 (FSU); FRANKLIN CO., E of Wright Lake SW of Sumatra, *Godfrey* 76,059 (FSU); LEON CO., Tallahassee, *Berg* s.n. (NY); S of Tallahassee, *Norris* 643 (TEX), W. of Tallahassee, *Godfrey* 75,743 (MO); LIBERTY CO., Bristol, *Mohr* s.n. (NY); WAKULLA CO., Apalachicola Nat'l Forest, Forest Rd.-113, *Godfrey* 76,245 (FSU).

10c & d. *Chrysopsis gossypina* subsp. *gossypina*.

Plants biennial or weakly perennial, surviving more than two seasons by means of basal rosettes developing at lower stem nodes. *Stems* erect to procumbent, 2–6 dm long, unbranched or branching, glabrous to densely woolly, sometimes stipitate-glandular. *Basal rosette leaves* oblanceolate, 3–10 cm long, apically dentate or entire, densely long-woolly, the hairs flagelliform. *Stem leaves* lanceolate or ovate-elliptic to oblanceolate, obtuse to acute, margins entire, sometimes ciliate, sparsely to densely woolly, sometimes glabrate with age. *Capitulescence* loosely corymbose-cymose, 1–10 (30) heads; *peduncles* glabrous to woolly, sometimes stipitate-glandular. *Involucres* 8–13 mm high, campanulate to hemispherical; *phyllaries* in 4–5 unequal series, glabrate to densely woolly, sometimes densely stipitate-glandular, usually some glands basally, linear-lanceolate to oblanceolate, 1–2 mm wide, appressed to recurved. *Ray florets* (9) 16–30, averaging about 21 per head, straps 7–12 mm long, 1–2.5 mm wide. *Disc florets* 6–7.5 mm long, lobes 0.5 mm long. *Cypselas* sparsely to moderately strigose, shallowly ribbed, 0–3 yellow to red-brown clavate, translucent ridges per side, 2–3 mm long; *pappus* double, the outer bristles short, the inner bristles 6–8 mm long. *Chromosome number*: $n = 9$.

The morphology and distribution of *Chrysopsis gossypina* subsp. *gossypina* are illustrated in Figs. 4A, 15A–F, and 16A–G. Three

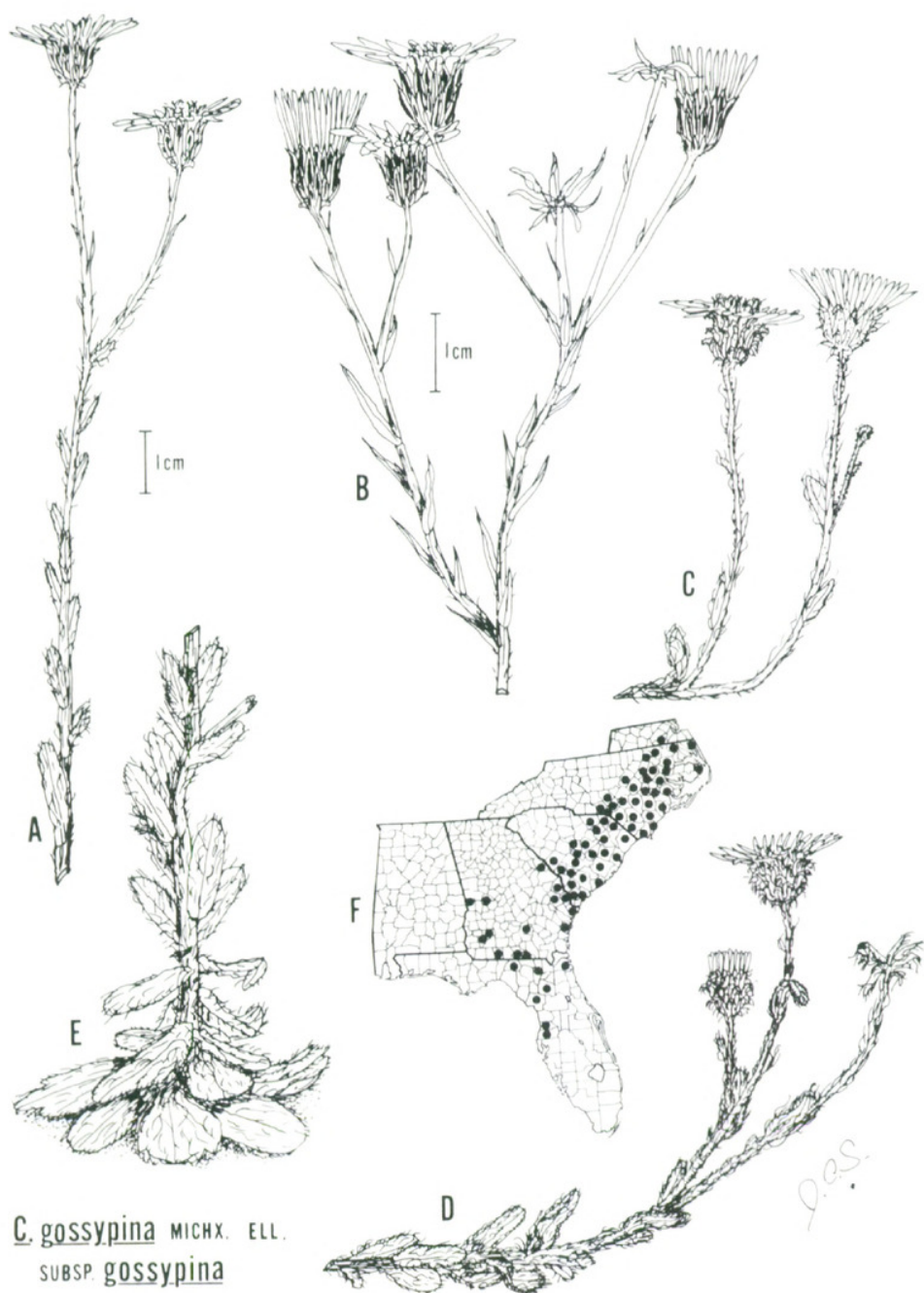


Figure 15. **Morphology and distribution of *C. gossypina* subsp. *gossypina*.** A. Flowering shoot of f. *gossypina* with sparsely pubescent, appressed phyllaries. B. Upper portion of a shoot of f. *trichophylla* with glabrous peduncles and phyllaries. C. Terminal portion of a decumbent shoot of f. *decumbens* with stipitate-glandular peduncles and phyllaries that are stipitate-glandular and spreading recurved. D. Procumbent shoot of f. *gossypina* with densely woolly peduncles and phyllaries, which are like the type collection. E. Lower stem and portion of shoot of either f. *gossypina* or f. *trichophylla*. F. County dot map of the distribution based on all collections seen.

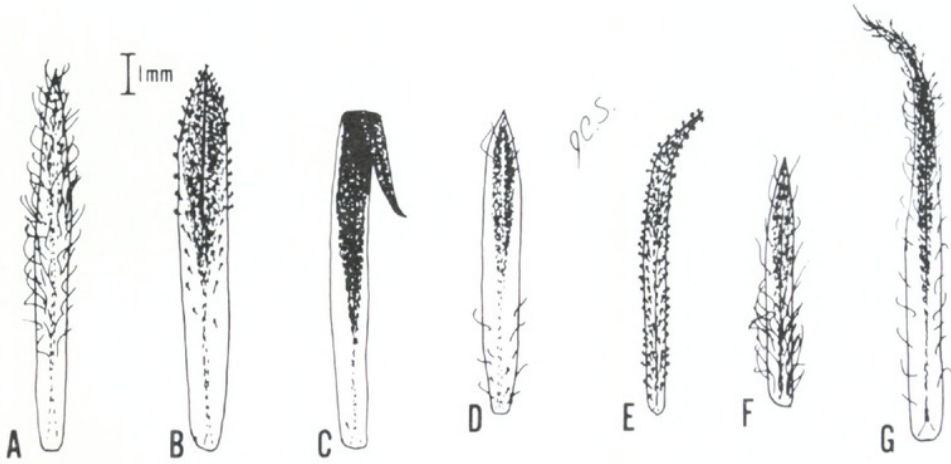


Figure 16. Phyllaries of *C. gossypina* subsp. *gossypina*. All are drawn to the same scale. A., D., F. & G.: *f. gossypina*; B. & E.: *f. decumbens*; C. *f. trichophylla*. A. Godfrey 48,681 (GA). B. Cronquist 4,728 (GH). C. Eggleston 4,951 (GH). D. Godfrey 48,681 (GA). E. Godfrey & Fox 48,674 (MO). F. Semple & Wunderlin 2,563 (WAT). G. Godfrey 76,102 (FSU).

forms have been given nomenclatural recognition. Intermediates are common and only the most pronounced variants are easily assigned to one of the named forms. The forms can occur in populations by themselves or in mixed populations. The intergradation is such that even varietal level recognition would be overemphasizing single characteristics.

The subspecies occurs in open sandy soils in pine woods and scruboak stands, disturbed sites along roadsides and naturally barren slopes. It blooms from September in the north to November in the south.

10c. *Chrysopsis gossypina* subsp. *gossypina* *f. gossypina*

Chrysopsis longii Fern., *Rhodora* **40**: 467. 1938. TYPE: Virginia, 7 mi S of Franklin, 7 & 8 Sept. 1937. Fernald & Long 7,664 (HOLOTYPE, GH!, ISOTYPES, NY!, PH!, US!).

Included in the type form are all individuals of the subspecies with some pubescence on the phyllaries and usually the peduncles as well. The phyllaries may be appressed to recurved. The heads are hemispherical to campanulate and vary greatly in size. The extremely woolly-pubescent morphotypes are most common in northern Georgia, the Carolinas, and Virginia. In Florida heads tend to be less pubescent. Leaf pubescence also varies from moderately to

densely woolly, the woolliest forms again occurring mostly in the north. Habit varies from erect to procumbent, sometimes with branches arising from anywhere between the base and the midstem region.

REPRESENTATIVE SPECIMENS. **Florida.** ALACHUA CO., SW of Gainesville, *Todsen & Arnold s.n.* (GA, TEX), Kanapaha, *Murill 399 & 400* (US); DUVAL CO., Jacksonville, *Curtiss 5,318* (F, GA, GH, NY, US); HERNANDO CO., *Cooley et al. 7,021* (USF); LEVY CO., *Garber s.n.* (F, GH, NY, PH, US); MADISON CO., SSW of Ellaville, *Kral 6,172* (GA, GH, USF); PASCO CO., Jessamine, *Barnhart 2,629* (F, NY). **Georgia.** BAKER CO., near Emory U., *Thorne 6,649* (GA); BULLOCK CO., Lott's Creek Church, *Boole 965* (GH); CHATHAM CO., Ft. Argyle Rd. *Mellinger s.n.* (GH); DOUGHERTY CO., Albany, *Eggleston 5,109* (NY); LOWNDES CO., S of Valdosta, *Faircloth 667* (GA, MO); MCINTOSH CO., Pocosin, NE of Ft. Barrington, *Bozeman 2,362* (GA); MUSCOGEE CO., *Smith s.n.* (GH, US); RICHMOND CO., Augusta, *Cuthbert 313* (NY); SCREVEN CO., Blue Springs, *Eyles 7,567* (GA, GH); TAYLOR CO., S of Butler, *Harper 2,240* (F, GH, MO, NY, US). **North Carolina.** BRUNSWICK CO.; Caswell Beach, *Godfrey 12,067* (GH), *Bell 16,297* (TEX); CUMBERLAND CO.; between Fayetteville & Jonesboro, *Radford & Stewart s.n.* (NY); CURRITUCK CO., N of Kitty Hawk, *Bright 15,996* (TEX); DARE CO., Kill Devil Hill, *Morton 11,999* (US); HARNETT CO., S of Spout Springs, *Godfrey 50,119* (F); HOKE CO., S of Antioch, *Godfrey & Fox 50,555* (NY); JOHNSTON CO., S of Benson, *Godfrey & Fox 48,704* (GH); LENOIR CO., SE of Kingston, *Randolph 569* (GH); NEW HANOVER CO., N of Carolina Beach, *Blake 12,436* (LL); ONSLOW CO., S of Jacksonville, *Moldenke 123* (MO, NY, PH); SCOTLAND CO., S of Aberdeen, *Godfrey 6,939* (GH); WAYNE CO., Goldsboro, *Godfrey 6,554* (GH). **South Carolina.** AIKEN CO., Aiken, *Eggleston 5,074* (GH, MO, NY); BAMBURG CO., WNW of Govan, *Ahles 37,644* (GA); CHARLESTON CO., S of Hollywood near Meggetts, *Blake 12,543* (TEX); CHESTERFIELD CO., W of McBee, *Godfrey 8,058* (F, MO, NY, PH, US); DARLINGTON CO., W of Hartville, *Norton 500* (US); GEORGETOWN CO.; S of Georgetown, *Blake 12,546* (LL); HORRY CO., between Ocean Drive and Myrtle Beach, *Godfrey & Boyce 50,451* (GH, NY); MARLBORO CO., N of Cheraw, *Godfrey & Fox 50,582* (NY, PH); ORANGEBURG CO., Eutawville, *Eggleston 4,961* (NY in part); RICHLAND CO., W of Clemson U. Ex. Station, *Crewz 871* (USF); SUMTER CO., Sumter, *Stone 409* (PH). **Virginia.** SOUTHAMPTON CO., S of Franklin, *Townsend 7,725* (F, GH, LL, MO, NY); *Fernald & Long 7,664* (MO), N of Smith's Ferry, *Fernald & Long 8,875* (GH, PH).

10d. *Chrysopsis gossypina* subsp. *gossypina* f. *trichophylla*
(Nutt.) Semple, Can. J. Bot. **58**: 147. 1980.

Inula trichophylla Nutt. Gen. N. Am. Pl. **2**: 150. 1818. TYPE: N. Carolina, *Nuttall s.n.* (HOLOTYPE, PH!).

Chrysopsis trichophylla (Nutt.) Ell., Sketch Bot. S.C. and Ga. **2**: 336. 1824.

Diplopappus trichophyllus (Nutt.) Hook. Compan. Bot. Mag. **1**: 97. 1836.

Heterotheca trichophylla (Nutt.) Shinnars, Field & Lab. **19**: 71. 1951.

Included in this form are plants with truly glabrous phyllaries and peduncles. The leaves are sparsely woolly to glabrate with some-

times ciliate margins. The heads are frequently large with the phyllaries appressed to slightly spreading at the tips. This morphotype is most common in the southern portion of the subspecies' range. The stems are erect and unbranched or branched below the middle.

This form has nearly always been given species status by authors, who Dress (1953) suggested "took up Nuttall's name" because they were unfamiliar with the *gossypina* complex and assumed it was a valid species. Dress placed the name in complete synonymy under his subsp. *gossypina*, not even giving the morphotype form status. Harms (1974b) felt that the *trichophylla* complex was one of the most difficult problems in *Chrysopsis* and one that was, even following his conspectus, in dire need of a careful study to resolve its phylogeny and nomenclature. Such a study has now been carried out and recognition of *trichophylla* as a form, the conclusion.

REPRESENTATIVE SPECIMENS. **Georgia.** DOOLY CO., Gum Creek, *Harper* 567 (F, GH, MO, NY, US); ECHOLS CO., S of Mayday, *Faircloth* 4,985 (GA, MO); LOWNDES CO., S of Naylor, *Faircloth* 4,915 (GA, MO). **North Carolina.** NEW HANOVER CO., Wilmington, *Bartram* s.n. (PH); BLADEN CO., White Lake, *Godfrey* 50,421 (F, NY, PH), near prison camp, *Godfrey & Fox* 49,499 (GH). **South Carolina.** BERKELEY CO., S of Monks Corner, *Ahles* 35,546 (FSU, GA, GH, USF); COLLETON CO., W of Hendersonville, *Leonard & Radford* 1,979 (LL, NY, TEX), *Bell* 4,634 (USF), *Ahles & Bell* 21,059 (GA); GEORGETOWN CO., S of Waverly Mills, *Radford* 31,266 (UNCC); ORANGEBURG CO., Eutawville, *Eggleston* 4,961 (NY).

The following specimens are intermediate between f. *gossypina* and f. *trichophylla*, or the duplicates include a range of variants between the two forms:

North Carolina. BLADEN CO., S of Ammon, *Ahles* 37,418 (NY). **South Carolina.** BERKELEY CO., Monks Corner, *Pennell* 4,887 (PH); ORANGEBURG CO., Eutawville, *Eggleston* 4,951 (F, GH, MO, NY, PH, US).

10e. *Chrysopsis gossypina* subsp. *gossypina* f. *ducumbens* (Chapm.)
Godfrey, *Rhodora* 51: 113. 1949.

Chrysopsis decumbens Chapman, Fl. S.U.S. 217. 1860. TYPE: Florida, *Chapman* s.n. (HOLOTYPE, NY!; ISOTYPES, F!, GH!, NY-ex Princeton Herbarium, PH-2 sheets! US-4 sheets!).

Chrysopsis arenicola Alexander in Small, Man. S.E. Fl. 1339. 1933.

This form occurs in scattered populations from St. Vincent Is., Gulf Co., Florida, to North Carolina, where it is commonly encountered in the fall line counties of the coastal plain. It

represents the extreme of the continuum in stipitate-glandularity of phyllaries and peduncles. The stems are decumbent with 1–10 heads in undamaged collections. The leaves are densely woolly. It is very similar morphologically to *Chrysopsis godfreyi* f. *godfreyi* which has a chromosome number of $n = 5$.

REPRESENTATIVE SPECIMENS. **Florida.** Type specimens. **North Carolina.** BRUNSWICK CO., Long Beach, *Godfrey & Boyce* 50,962 (GH, NY, PH, TEX); MOORE CO., W of Eastwood, *Godfrey* 50,713 (GA, GH, NY); NEW HANOVER CO., Wilmington, *Canby s.n.* (NY in part), *Wherry s.n.* (LL); RICHMOND CO., NE of Rockingham, *Cronquist* 4,728 (GA, GH, NY, PH); WAKE CO., between Fugay Springs and Duncan, *Godfrey & Fox* 48,674 (MO).

The following collection has traits intermediate between f. *trichophylla* and f. *decumbens*.

Georgia. LAURENS CO., S of Dublin, *Godfrey* 50,791 (GA, MO, NY).

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DEPARTMENT OF BIOLOGY
UNIVERSITY OF WATERLOO
WATERLOO, ONTARIO
CANADA, N2L 3G1



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