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DOI

[10.2307/2445740](https://doi.org/10.2307/2445740)

Publication date

1994

Published in

American Journal of Botany

[Link to publication](#)

Citation for published version (APA):

Battjes, J., Chambers, K. L., & Bachmann, K. (1994). Evolution of microsporangium numbers in *Microseris* (Asteraceae: Lactuceae). *American Journal of Botany*, 81, 641-647.
<https://doi.org/10.2307/2445740>

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American Journal of Botany, Vol. 81, No. 5. (May, 1994), pp. 641-647.

Stable URL:

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EVOLUTION OF MICROSPORANGIUM NUMBERS IN *MICROSERIS* (ASTERACEAE: LACTUCEAE)¹

JOHANNES BATTJES, KENTON L. CHAMBERS,² AND
KONRAD BACHMANN³

Hugo de Vries Laboratory, University of Amsterdam, Kruislaan 318,
1098 SM Amsterdam, The Netherlands

The genus *Microseris* contains species with disporangiate stamens and species with tetrasporangiate stamens. We determined the number of microsporangia per stamen in serial sections of heads from all 13 species of *Microseris*, its close relative *Uropappus lindleyi*, and the two allopolyploid species of *Stebbinsoseris*. Four *Microseris* species, three diploid and one tetraploid, have two microsporangia per stamen; all other species investigated have four. The most parsimonious assumption is that the disporangiate condition is derived and arose once in the evolution of *Microseris*. The inheritance of the number of microsporangia per stamen in crosses between *M. bigelovii* (disporangiate) and *M. douglasii* (tetrasporangiate) was determined. Segregation of microsporangium number per stamen in F₂s derived from these crosses is quantitative rather than Mendelian. The average number of microsporangia per stamen in the F₂ plants ranges from 2.0 to 4.0. There is a predominance of tetrasporangiate stamens in the F₁ and in most F₂ plants. The observed pattern of inheritance suggests a major gene with dominance and quantitative modifiers.

The number of microsporangia per stamen shows little variation in flowering plants. About 90% of the species have four microsporangia, the remainder having either more or less (Endress and Stumpf, 1990). Both the constancy of the tetrasporangiate condition and deviations from it have been explained by functional constraints. Endress and Stumpf (1990) relate the occurrence of four microsporangia per stamen to the efficiency of the opening mechanism. According to these authors, deviating numbers often occur in species with specialized pollination mechanisms. For example, disporangiate anthers can occur in connection with mucilaginous pollen masses, secondary pollen presentation, cleistogamy, or opening of the anthers by means of valves. In addition, it has been suggested that in the Asteraceae, disporangiate stamens occur mostly in autogamous species (Thiele, 1988). However, there are many selfing asteracean species with four microsporangia (Thiele, 1988). It is unknown to what extent developmental factors influence the evolution of microsporangium numbers.

The genus *Microseris* has 13 species and contains both selfing and outcrossing species (Chambers, 1955). It is closely related to *Uropappus lindleyi*, and the two tetraploid species of *Stebbinsoseris* are the allopolyploid derivatives of *Uropappus lindleyi* and a *Microseris* species (Jansen et al., 1991). Some of the selfing *Microseris* species are disporangiate (Thiele, 1988). Therefore, the genus *Microseris* can serve as a microevolutionary model of how numbers of microsporangia evolve and how these numbers are related to the evolution of floral syndromes related to autogamy. Some of the selfing *Microseris* species are partly interfertile (Chambers, 1955; Vlot et al., 1992). A genetic analysis of a cross between these species would yield insight as to how the tetrasporangiate condition is determined. In this paper we survey all *Microseris* species

and allopolyploid derivatives in order to confirm that the disporangiate condition is a derived character in *Microseris*. In addition we analyze the genetic complexity of the derived condition in two crosses between a disporangiate and a tetrasporangiate species.

MATERIALS AND METHODS

Plant material—The following species and accessions were studied from greenhouse material (strains) or herbarium collections (vouchers):

Microseris acuminata (strains E62, E66; vouchers 407, 1597); *M. bigelovii* (strains C94, D33b); *M. borealis* (from Mt. Hood, Oregon); *M. campestris* (strains E41, E65; vouchers 2139, 2204, 3705); *M. douglasii* (strains A26, B14, C57b, D57, E34a, E43b, E55a, E59b, E63a, E73c); *M. elegans* (strains D02, D07, D08); *M. howellii* (voucher A268); *M. laciniata* (voucher A260); *M. nutans* (strain C06); *M. paludosa* (voucher A261); *M. pygmaea* (strains A92, C96); *M. scapigera* (strains D91, F01); *M. sylvatica* (vouchers A269, 2164); *Stebbinsoseris decipiens* (strain D60); *S. heterocarpa* (strain D61); and *Uropappus lindleyi* (strain A30). Strains are maintained at the University of Amsterdam; vouchers are herbarium collections by K. L. Chambers housed at Oregon State University (OSC). Three crosses were obtained by hand pollination: D17 and H27 (both crosses between *M. douglasii* strain B14 as pollen acceptor and *M. bigelovii* strain C94), and D19 (between *M. bigelovii* strain C94 as pollen acceptor and *M. douglasii* strain A26). We have studied three F₁ individuals of cross H27 and the F₂ families from D17 and D19. F₂ families were derived from the F₁ by spontaneous selfing. All lines were grown in the greenhouse in various years, and heads containing developing flowers were collected, fixed, and stored in 70% ethanol or Craf III, in accord with standard cytological procedures.

Anatomical methods—Herbarium material was soaked overnight in 10% NH₃. Both the herbarium material and

¹ Manuscript received 28 June 1993; revision accepted 29 October 1993.

² Current address: Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331-2910.

³ Author for correspondence.

the alcohol collections were dehydrated in a graded 1-butanol series and embedded in glycol methacrylate. Sections (5 to 10 μm) were made with a rotary microtome and stained with the periodic acid-Schiff's reaction and toluidine blue O, in accord with standard anatomical procedures.

Scoring—We examined one head per collected plant. Since the microsporangia open early in flower development, only young buds have intact microsporangia. From the herbarium material, only mature heads were studied. Following Thiele (1988), the number of microsporangia per anther in this material was judged from the presence of the preserved endothecium of the adaxial microsporangia (Fig. 1). Tetrasporangiate anthers have an adaxial (ventral) and an abaxial (dorsal) endothecium, and the pollen sacs open with a slit between the adaxial and abaxial endothecia. As a result, when the pollen sacs have opened, the abaxial endothecium is clearly distinct from the adaxial (Fig. 1). Disporangiate asteracean anthers have the abaxial endothecium but lack the adaxial endothecium. Therefore, according to Thiele (1988), the presence of the adaxial endothecium indicates a tetrasporangiate rather than a disporangiate anther. We confirmed that disporangiate *M. elegans* anthers indeed lack the adaxial endothecium, whereas it is distinctly visible in tetrasporangiate *M. douglasii* anthers. Since there was little variation among the flowers of one head, most samples were classified as either di- or tetrasporangiate. For the hybrid lines we scored each head as follows: 20 florets in each head from the periphery to the center were examined in about ten sections at various levels. In each head, all microsporangia present in one or more sections were counted and divided by the total number of stamens, yielding the average number of microsporangia per anther.

Pollen counts—For the diploid annual species *M. douglasii*, *M. elegans*, *M. bigelovii*, and *M. pygmaea*, we counted the number of pollen per microsporangium in whole anthers under a light microscope. The majority of *Microseris* florets contains one ovule and five anthers, and two or four microsporangia per anther, i.e., a ratio of ten, respectively, 20 microsporangia per ovule. The pollen-ovule ratios therefore were estimated by multiplying the number of pollen grains per microsporangium by ten in the disporangiate species. For the estimation of pollen-ovule ratios in tetrasporangiate *M. douglasii*, pollen grain numbers of adaxial and abaxial microsporangia were added and then multiplied by ten.

RESULTS

Anther anatomy of *Microseris*—The variability of anther structure in *Microseris* is illustrated in Figs. 1–8. In artificial crosses, anther forms can be encountered that deviate from anther morphology in natural populations or their greenhouse-grown offspring (Figs. 9–12). Anther anatomy of *Microseris* basically resembles that of other asteracean species (Pullaiah, 1984; Thiele, 1988). The anthers contain two or four microsporangia, inserted laterally of the connective (Figs. 2–4). Depending on de-

velopmental stage, the center of each microsporangium contains pollen mother cells or pollen grains. The layer of pollen mother cells can vary considerably in size among species. The outcrossing *M. nutans* shows about two pollen mother cells per microsporangium in cross sections and about 50 in longitudinal sections (Figs. 4, 5). Microsporangia of selfing *M. douglasii* contain between three and five pollen mother cells in a single row (Fig. 6). The pollen mother cells are enclosed by the tapetum. Toward the periphery of the anther, the tapetum is covered by a middle layer, endothecium, and epidermis (Fig. 4). Each of these layers has a thickness of one cell. The endothecium cells do not differ in size from adjacent middle layer and epidermis cells during early anther development (Fig. 4). At about the time of the first pollen mitosis, the endothecial cells enlarge (Fig. 8) and form radial wall thickenings (Pullaiah, 1984). The endothecium persists in mature flowers, in which the tapetum and middle layer are not recognizable anymore (Fig. 1). In comparison with tetrasporangiate stamens, disporangiate stamens lack the adaxial microsporangia (Figs. 7, 8), and accordingly the adaxial part of the endothecium. In progenies from artificial intraspecific crosses, between two and four microsporangia can develop per anther (Figs. 9–12). When the number of microsporangia per anther in these progeny plants is two or three, there is always undifferentiated tissue at the site of the missing microsporangia (Figs. 11, 12). This is in contrast with the parental disporangiate phenotype, which never shows such undifferentiated tissue adaxial of the two microsporangia (Fig. 7).

Phylogeny of microsporangium numbers—Most specimens from natural populations or their greenhouse-grown offspring could be categorized as either di- or tetrasporangiate, because no deviations from two or four pollen sacs per anther occurred (Figs. 7, 8). Only one collection of disporangiate *M. pygmaea* (A92) showed irregular adaxial microsporangia in the lowest part of the anther (Figs. 2, 3). In one herbarium collection of *M. acuminata* the adaxial endothecium was not always visible, whereas the other samples of the species contained mostly tetrasporangiate stamens. This may be related to the observation that in some of the serial sections of *M. acuminata* with intact microsporangia, only one adaxial microsporangium was present at a median position, leaving no space for an endothecium.

Numbers of microsporangia per anther for each species are given in Fig. 13. When multiple populations from the same species were studied, all populations had the same number of microsporangia. The phylogenetic relationships among the species in Fig. 13 are based on chloroplast DNA data (Wallace and Jansen, 1990) and morphology (Chambers, 1955). All perennial diploid *Microseris* species have four microsporangia per anther. The monophyly of this group is clearly demonstrated by chloroplast DNA studies (Wallace and Jansen, 1990). The four annual diploid *Microseris* species also are monophyletic for chloroplast DNA when tetraploids are not considered, but they differ in the number of microsporangia per anther. Of the four annual diploids, *Microseris douglasii* has four microsporangia, whereas *M. elegans*, *M. bigelovii*, and *M. pygmaea* have two microsporangia. The most parsimonious assumption is that the ancestral condition in *Mi-*

Figs. 1–6. Microsporangium variability in *Microseris*. Bar = 50 μ m. 1. *M. laciniata*, tetrasporangiate, herbarium sample of dehiscent anther. In addition to the abaxial endothecium (AbE) and the connective (C), the adaxial endothecium (AdE) is clearly visible. P, pollen grain. 2. *M. pygmaea* (strain A92), disporangiate upper part of floret. C, connective; L, ligule; M, microsporangium; PP, pappus part; S, style. 3. Same capitulum, lower part of floret. In addition to the two microsporangia (M), adaxial tissue (Ad) is incompletely differentiated into microsporangia. 4. *M. nutans*, tetrasporangiate anthers with a pair of abaxial (AbM) and adaxial (AdM) microsporangia inserted laterally of the connective (C). From the center toward the periphery the microsporangium consists of pollen mother cells (PMC), tapetum (t), middle layer (m), endothecium (en), and epidermis (ep). 5. *M. nutans*, longitudinal section. More than 50 pollen mother cells (PMC) per microsporangium can be found. 6. *M. douglasii* (strain B14) tetrasporangiate, longitudinal section. Four pollen mother cells (PMC) per microsporangium.

croseris is tetrasporangiate and that the disporangiate condition originated once among annual diploid species. This agrees with the classification by Chambers (1955), who separated *M. douglasii* from the other diploid annual *Microseris* species on morphological grounds.

All tetraploid *Microseris* and *Stebbinsoseris* species are closely related to at least one diploid annual *Microseris* species (Chambers, 1955; Wallace and Jansen, 1990; Jansen et al., 1991). *Microseris campestris*, which unites morphological characters of both *M. elegans* (disporangiate)

Figs. 7–12. Genetics of microsporangium numbers in *Microseris*. Bar = 50 μ m. 7. *M. bigelovii* (strain C94). All anthers contain two microsporangia (M) per anther. 8. *M. douglasii* (strain B14). All anthers contain four microsporangia (M). The endothelial cells (e) are enlarged relative to surrounding tissue. 9. F1 of the cross *M. douglasii* $\times$ *M. bigelovii* (H27). Most anthers contain four microsporangia (M). 10–12. F2 of the cross *M. bigelovii* $\times$ *M. douglasii* (D19). 10. Floret from a head with exclusively four microsporangia (M) per anther. 11. Floret with two, three, and four microsporangia (M) per anther. In anthers with two and three microsporangia, there are several undifferentiated cell layers present at the adaxial side (Ad) of the anther. 12. Floret from a head with exclusively two microsporangia (M) per anther. In comparison with parental *M. bigelovii* (Fig. 7), more tissue is present adaxially (Ad) of the microsporangia (M).

and *M. douglasii* (tetrasporangiate), is disporangiate. *Stebbinsoseris decipiens*, closely related to the disporangiate *M. bigelovii*, in contrast, is tetrasporangiate, as are the other tetraploids.

Inheritance—The parental strains of the crosses between *M. bigelovii* and *M. douglasii* have two and four microsporangia per anther, respectively (Figs. 7, 8). Three F1 plants all have on average slightly less than four mi-

Fig. 13. Simplified phylogeny of *Microseris* and its derived polyploids. The two deepest branches among the diploid species are based on chloroplast DNA (Wallace and Jansen, 1990). Relationships between diploids and tetraploids are based on morphological data (Chambers 1955). Nomenclature from Jansen et al. (1991). Numbers after species names indicate the number of microsporangia per anther. * = outcrossing perennials; ** = selfing annuals.

crosporangia per anther, indicating dominant inheritance of at least some of the genes involved (Fig. 9). The two F₂ hybrid progeny families were derived from the same *M. bigelovii* parental strain but from two different *M. douglasii* strains. Nevertheless, the pattern of inheritance is essentially the same in both families (Fig. 14). A large proportion of F₂ plants has precisely four microsporangia per anther or slightly less (3.81–4.0 class, Fig. 10). The remainder, about one-half of the plants, shows much variation in microsporangium numbers. Two, three, or four microsporangia may be present in the anthers of one floret (Fig. 11). In almost all cases with two or three microsporangia per anther, one or two of the adaxial sporangia have disappeared. The average number of microsporangia in these plants varies between 2.0 and 3.8 (Fig. 14). The frequency histograms of average microsporangium numbers per plant in the F₂ families are two-peaked, with a minimum number of heads in the 3.01–3.20 class when observations from both families are pooled. The occurrence of 17 heads with less than 3.0 microsporangia per head and 48 with more does not significantly deviate from a 1:3 segregation ($G = 0.223$). Only one F₂ plant from a total of 75 in two F₂ families has precisely 2.0 microsporangia per anther (Fig. 12). This disporangiate F₂ plant does not exactly resemble the *M. bigelovii* stamen, since the anthers do have sterile adaxial lobes, whereas the adaxial border of *M. bigelovii* anthers is straight and smooth (Fig. 7).

Number of pollen grains per microsporangium—Numbers of pollen grains per microsporangium were determined for the four annual diploid species. The lowest average number of pollen grains per microsporangium was found in *M. elegans*, the highest in *M. bigelovii*, both disporangiate species. *M. douglasii* has the highest number of pollen grains per flower, due to the fact that it has four

Fig. 14. Average number of microsporangia per anther in crosses between *M. bigelovii* (disporangiate) and *M. douglasii* (tetrasporangiate).

microsporangia (Table 1). The difference between the annual species and the perennial *M. nutans* in amount of sporogenic tissue is considerable: *M. nutans* can have more than 50 pollen mother cells per microsporangium, compared to a maximum of eight to ten in the diploid annuals (Figs. 4–6).

DISCUSSION

Variation in microsporangium numbers in *Microseris* was first reported among three annual species by Thiele (1988). Here, we present additional information on all species of *Microseris* and its allopolyploid derivatives. In *Microseris*, the dichotomy between diploid annual species and diploid perennials is well established both by cytology, morphology, growth form, and chloroplast DNA markers (Chambers, 1955; Wallace and Jansen, 1990). With respect to the phylogenetic relationships among diploid annuals, molecular and morphological data contradict each other. Morphologically, *M. douglasii* differs from the other three diploid annuals by the structure of its achenes and pappus. The DNA data, however, are as yet

TABLE 1. Average number of pollen grains per microsporangium and estimated pollen-ovule ratio.^a

Species (strain)	N	Average $\pm$ SD (abaxial sporangia)	Average $\pm$ SD (adaxial sporangia)	Pollen-ovule ratio
<i>M. pygmaea</i> (A92)	18	20.6 $\pm$ 3.70		206
<i>M. pygmaea</i> (C96)	9	26.8 $\pm$ 4.50		268
<i>M. elegans</i> (A24)	4	8.00 $\pm$ 0.00		80
<i>M. elegans</i> (D05)	14	9.00 $\pm$ 2.32		90
<i>M. bigelovii</i> (D58)	8	23.0 $\pm$ 4.24		230
<i>M. bigelovii</i> (D43)	10	31.8 $\pm$ 3.19		318
<i>M. douglasii</i> (E63)	4	23.5 $\pm$ 2.38	14.3 $\pm$ 3.50	378
<i>M. douglasii</i> (C57)	4	18.8 $\pm$ 3.40	14.8 $\pm$ 2.22	335

^a N, number of observations; SD, standard deviation.

inconclusive. *Microseris douglasii* appears in two different branches of the chloroplast DNA tree among the other diploid annuals (Wallace and Jansen, 1990). Nuclear DNA markers point to a close relationship between *M. bigelovii* and *M. pygmaea*, but the relationship between these two and *M. douglasii* and *M. elegans* remains unresolved (van Houten, Scarlett, and Bachmann, 1993). For this reason we studied more collections from *M. douglasii* than from the other species, selecting morphologically divergent biotypes from various geographical regions. All these *M. douglasii* samples have four microsporangia per anther. The tetrasporangiate stamen clearly distinguishes *M. douglasii* from the other diploid annuals, in agreement with morphological characters rather than DNA markers.

The tetraploid *M. campestris* is morphologically intermediate between the disporangiate *M. elegans* and the tetrasporangiate *M. douglasii* (Chambers, 1955). Assuming that (close relatives of) these species are the diploid ancestors of *M. campestris*, it is peculiar that it has two rather than four microsporangia, given the dominance of the latter number in artificial crosses. The ancestry of *M. campestris* needs a reevaluation in the light of these results.

The number of microsporangia is essentially a two-state character in *Microseris* phylogeny. This pattern of natural variation contrasts with the segregation in hybrid progenies from a cross between a disporangiate and a tetrasporangiate species. The inheritance in the F2 behaves as a quantitative character rather than a Mendelian one. We did not study heritabilities and therefore we do not know which part of the quantitative variation is environmentally induced. Nevertheless, we can draw some preliminary conclusions on the inheritance. Only one in 75 F2 plants equals the lower parental score in microsporangium numbers. This comes closest to a 63:1 ratio, expected when three genes with recessive alleles for the *M. bigelovii* phenotype are involved. Even more genes may be required to diminish the sterile adaxial lobes still present in this disporangiate F2 plant. On the other hand, the distribution of average microsporangium numbers in the F2 is bimodal. The ratio of the areas under the peaks is approximately 1:3, suggestive of a single gene effect. Thus, the inheritance of microsporangium numbers is oligogenic or polygenic, but one major gene with dominant inheritance may account for much of the genetic variation in the F2. A similar pattern of inheritance was observed for the number of pappus parts per fruit, three vs. five, in the same *M. douglasii* $\times$ *M. bigelovii* cross as studied here

(Vlot et al., 1992). In that study, the major gene effect was tightly linked to a nuclear DNA marker. Another example of a cross between species with mutually exclusive numbers of parts is that between *M. pygmaea* with ten pappus parts per fruit and *M. bigelovii* with five pappus parts (Chambers, 1963). Variation in the F2 and later generations was continuous and determined by multiple genes. The parental ten pappus part genotype was never recovered in selection experiments (Zentgraf et al., 1984). *Plantago maritima* has races with predominantly two ovules and races with typically four ovules. In an F2 derived from a hybrid between plants with two and four ovules, segregation was monogenic (Gregor, 1939). Gottlieb (1984) supposes that differences between plant species in structure, shape, orientation, and presence vs. absence of organs are often governed by one or two genes. Differences in dimensions, weight, and number usually are influenced by multiple genes. Hilu (1983) and Bachmann (1983) also describe major gene effects for many morphological and quantitative differences among plant species. According to these authors, these effects may be quantitatively modified by several or many genes with small effect. The segregation pattern reported here fits well into the last hypothesis. Small modifying gene effects seem to be essential to maintain a regular di- or tetrasporangiate anther. All conclusions on the genetics of microsporangium numbers reported here need further testing.

Disporangiate stamens occur in various tribes of the Asteraceae (Pullaiah, 1984; Thiele, 1988; Endress and Stumpf, 1990). In most cases, the adaxial sporangia have been lost (Endress and Stumpf, 1990) although in *Conyza ambigua* the abaxial sporangia seem to be absent (Sarma, 1986). As in most Asteraceae, the adaxial sporangia in disporangiate *Microseris* are reduced. This can be inferred from *M. pygmaea* A92, which has traces of adaxial sporangia at the bottom of the anthers, and from di- or trisporangiate F2 plants that always lack adaxial sporangia. Trisporangiate stamens have been observed in *Senecio vulgaris* (Endress and Stumpf, 1990) and *Youngia japonica* (Kaul, 1973 cited in Pullaiah, 1984). Although trisporangiate stamens are found in artificial *Microseris* crosses, they do not occur in inbred lines and herbarium material collected in natural populations. The one exception is *M. acuminata*, which in some stamens of a single capitulum may have only one median adaxial microsporangium. It is tempting to speculate that in most disporangiate *Microseris* species, modifying genes completely suppress the formation of adaxial microsporangia. In trisporangiate *Senecio vulgaris* and *Youngia japonica*, as well as in *M. pygmaea* A92, then, such modifiers have not evolved.

Selving plants on the average have a lower pollen-ovule ratio than outcrossing plants (Cruden, 1977). The reduction of microsporangium numbers in some autogamous Asteraceae (Thiele, 1988) would be consistent with this trend if microsporangium numbers are correlated with pollen production. Our limited data indicate that there is much variation in pollen production among microsporangia in the same flower or head. Tetrasporangiate *M. douglasii* has a higher pollen-ovule ratio than the closely related disporangiate species *M. bigelovii*, *M. elegans*, and *M. pygmaea*. Variation among these disporangiate lines is considerable and almost overlaps with ratios in *M. douglasii*. The difference in pollen number between the

diploid annuals and the diploid perennial *M. nutans*, caused by a difference in the number of pollen mother cells per sporangium, is much more pronounced. Both a reduction in microsporangium numbers and in the amount of sporogenous tissue per sporangium are also observed in *Collomia grandiflora*. In this species, disporangiate cleistogamous flowers occur in the same inflorescence as tetrasporangiate chasmogamous flowers. The reduction in microsporangium number is associated with a tenfold reduction in the number of pollen grains and an associated reduction in sporogenous tissue per microsporangium (Lord, Eckard, and Crone, 1989). In *Microseris* we can distinguish two steps in the evolution of pollen grain numbers. A difference in anther length has led to a more than tenfold difference in pollen production per microsporangium between some selfing and outcrossing species. The reduction in microsporangium numbers per anther results in a less dramatic difference in pollen production among the selfing species. Whether this latter minor difference has had effects on fitness, mediated by for example the degree of cross pollination or developmental speed of florets, remains to be determined.

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