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CHROMOSOME NUMBERS IN COMPOSITAE. IV. AMBROSIEAE[1]

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ABSTRACT

New chromosome observations are reported for 30 species and varieties from 4 genera of Ambrosieae: *Ambrosia* (including *Franseria*), *Dicoria*, *Hymenoclea* and *Iva*. Neither polyploidy nor aneuploidy is known in the genera *Dicorea*, *Hymenoclea* or *Xanthium*. Aneuploid reduction appears to have played a role in the genome evolution of several species of *Iva* and *Ambrosia*. Polyploid species occur in both *Iva* and *Ambrosia* and polyploid series exist for at least 5 species or species aggregates of the latter. All available evidence indicates that the primitive chromosome number for the tribe is $x = 18$, differentiation and speciation having occurred at this level, which is here termed diploid. The group, however, must ultimately have been of polyploid origin from forms with $x = 9$.

THIS is the fourth in a recent series of papers dealing with chromosome numbers in various tribes of the Compositae. Materials and methods are generally those discussed in earlier contributions to this series, the most recent of which is Ornduff et al. (1963). Procedural details have varied somewhat since work was carried out independently by the various workers. We are indebted to Dr. Arthur Cronquist for his determination of *Iva nevadensis*, to Dr. A. G. Norman, Director of the University of Michigan Botanical Gardens, for arranging maintenance of many of the plants for which observations are reported, and to Dr. W. H. Wagner, Jr. and Dr. B. L. Turner for their reviews of the manuscript.

The ragweeds and their relatives are commonly classified as a subtribe, Ambrosiinae, of the tribe Heliantheae, but a number of attributes, present in all of the genera incorporated (*Iva*—including *Leuciva*, *Oxytenia*, *Chorisiva* and *Cyclachaena*, *Dicoria*, *Euphrosyne*, *Hymenoclea*, *Xanthium*, and *Ambrosia* [including *Franseria*]), may warrant elevation of the group to the position of a tribe within the present tribal structure of the Compositae. These include: (1) the development of anemophily and its associated modification and reduction of capitula and florets; (2) the nodding insertion of staminate or androgynous heads on the inflorescence axis; (3) the indeterminant development pattern of the racemose or spicate inflorescences; (4) the weakly connate nature of the stamens of staminate florets; (5) the development of bladder-like air chambers in the intercolpoidal regions of the exine of the pollen wall. As a group, these plants appear to be related to both the Heliantheae and the Anthemideae but are removed from both through specialization (Payne, 1963). For the present, therefore, we have deemed it the best course to recognize the group as a distinct tribe, the Ambrosieae, a treatment which follows the precedents of Cassini (1834) and Delpino (1871), and which agrees in general meaning with the remarks or treatments of Bentham (1873), Small (1913), Rydberg (1922) and others.

The occurrence of hybridization, evident cross-relationships in several parts of both genera, and poor morphological distinctions (Gebben, Payne, and Wagner, 1962; Payne, 1962, 1963) all lead the authors to accept the proposal of Shinners (1949) that *Franseria* and *Ambrosia* are congeneric. Detailed evidence for this and a conspectus of the combined genus, *Ambrosia*, will be presented in a forthcoming paper by Payne. For the purposes of this paper we shall treat all species for which binomials are available under *Ambrosia* and leave the remainder, for the time being, under *Franseria*.

Table 1 includes, unless otherwise noted, original, meiotic chromosome counts for listed members of Ambrosieae. Meiotic irregularities are indicated by footnotes. Collection numbers preceded by *P* are by Payne and by *R* are by Raven. Herbaria in which voucher specimens are deposited are indicated immediately after the collection numbers. Camera lucida drawings of previously unreported chromosome complements, representative for 17 clones or populations of 4 ragweed species, are shown in Fig. 1.

With the material in Table 1, some of which repeats or verifies counts reported in the literature, chromosome counts are available for members of all 6 of the genera currently recognized in the Ambrosieae, except for the monotypic, Mexican genus, *Euphrosyne*. In the genus *Iva* (including *Oxytenia*, etc.) numbers have been reported for 14 of the 19 species recognized by Jackson (1960). Counts are available for all 3 species of *Hymenoclea*, for 1 of the 4 closely

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TABLE 1. *Cytological observations for Ambrosieae*

Species	Gametic chromosome number	Locality, collection and voucher location
Ambrosia (*Franseria*)		
A. acanthicarpa	18[a]	Madera Co., Calif., *P-AHI-2323* (MICH; garden progeny)
	18	San Bernardino Co., Calif., *R-16678* (RSA)
	18	Washoe Co., Nev., *R-16785* (MICH)
F. ambrosioides	18[a]	Maricopa Co., Ariz., *P-2699* (MICH)
	18	Sonora, Mexico, *R-11687* (UC)
A. artemisiifolia	18[a]	Laramie Co., Wyo., *P-AOT-3034* (MICH; garden progeny)
A. a. "var. *maritima*"	18[a]	Nancy, France, *P-AIR-2324* (MICH; garden progeny)
A. bryantii	18[a]	Baja California, Mexico, *Porter 456* (MICH)
F. camphorata	36(G)[b]	San Luis Potosí, Mexico, *P-4175* (MICH)
A. canescens	18(C)[b]	Aguascalientes, Mexico, *P-4051* (MICH)
F. chamissonis	18[a]	Marin Co., California, *P-2735* (MICH)
	18	San Francisco, Calif., *R-16558* (MICH)
F. c. ssp. *bipinnatisecta*	18[a]	Marin Co., Calif., *P-2733* (MICH)
	18	San Francisco, Calif., *R-16559* (MICH)
F. chenopodiifolia	36[c]	Baja California, Mexico, *R-12197* (UC)
	36[d]	Baja California, Mexico, *R-17038* (UC)
A. chieranthifolia	36(P)[b]	Nueces Co., Texas, *P-AVG-4356* (MICH; garden progeny)
A. confertiflora	36	Los Angeles Co., Calif., *R-16785* (JEPS)
	36	Los Angeles Co., Calif., *R-16844* (JEPS)
A. c. var. *tenuifolia*	54(F)[b]	Zacatecas, Mexico, *P-4115* (MICH)
	36[a]	Los Angeles Co., Calif., *P-AIG-2984* (MICH; garden progeny)
A. cumanensis	18(D)[b]	Vera Cruz, Mexico, *P-3841* (MICH)
A. deltoidea	18[e]	Sonora, Mexico, *R-14807* (MICH)
A. eriocentra	18	San Bernardino Co., Calif., *Balls 22495* (RSA)
A. grayi	18[a]	McPherson Co., Kans., *P-2621* (MICH)
A. hispida	72[a]	Monroe Co., Fla., *P-AHK-3142* (MICH; garden progeny)
F. ilicifolia	18[a]	Yuma Co., Ariz., *P-AJO-3089* (MICH; garden progeny)
	18	Sonora, Mexico, R-14807 (MICH)
A. peruviana	36[a]	Jamaica, West Indies, *P-AIU-3143* (MICH; garden progeny)
A. psilostachya	36[a]	Bay Co., Mich., *P-1619* (MICH)
	36[a]	Tulsa Co., Okla., *P-ALC-3347* (MICH; garden progeny)
	36(E)[b]	Querétaro, Mexico, *P-3867* (MICH)
	36(H)[b]	McPherson Co., Kans., *P-AJC-4225* (MICH; garden progeny)
	36(I)[b]	Zacatecas, Mexico, *P-4122* (MICH)
	36(J)[b]	Durango, Mexico, *P-4141* (MICH)
A. psilostachya	54(K)[b]	Lamar Co., Texas, *P-3649* (MICH)
	54(L)[b]	Coahuila, Mexico, *P-3768* (MICH)
	54(M)[b]	Coahuila, Mexico, *P-3769* (MICH)
	54(N)[b]	Yolo Co., Calif., *P-ARM-4226* (MICH; garden progeny)
	54(O)[b]	Summitt Co., Utah, *P-AKS-4227*; (MICH; garden progeny)
A. psilostachya	72[a]	Yolo Co., Calif., *P-ALE-2975* (MICH; garden progeny)
A. pumila	36[a]	San Diego Co., Calif., *P-2718* (MICH)
A. trifida	12[a]	Leiden, Netherlands, *P-AHN-2319* (MICH; garden progeny)
	12[a]	Lenawee Co., Mich., *P-AHU-2525* (MICH; garden progeny)
	12(A)[b]	Dallas Co., Texas, *P-3654* (MICH)
	12(B)[b]	Dallas Co., Texas, *P-3658* (MICH)
Dicoria		
D. canescens	18	Riverside Co., Calif., *R-16840* (JEPS)
Hymenoclea		
H. monogyra	18	San Bernardino Co., Calif., *R-16677* (JEPS)
H. pentalepis	18	San Bernardino Co., Calif., *Munz 21518* (RSA, garden progeny)
H. salsola	18	Riverside Co., Calif., *R-11414* (MICH)
Iva		
I. annua	17[a]	Athens Co., Ohio, *P-1944* (MICH)
I. axillaris ssp. *robustior*	18	Lassen Co., Calif., *R-13265* (JEPS)
	18	Elko Co., Nev., *R-13517* (JEPS)
	$2n = 54$[f]	Douglas Co., Nev., *R-14292* (MICH)
	$2n = 54$[f]	Fresno Co., Calif., *R-15096* (MICH)

[a] These counts have appeared previously in Gebben, Payne, and Wagner (1962) and in Payne (1962). They are reiterated here because of the general non-availability of those reports.

[b] Letters refer to drawings in Fig. 1.

[c] Plus an extra pair of chromosomes.

[d] Plus a fragment.

[e] Plus 2 unpaired univalents.

[f] With a high proportion of trivalents. *R-14292* had up to 13 trivalents, 5 pairs, and 5 univalents (cf. Bassett, Mulligan, and Frankton, 1962, p. 1246).

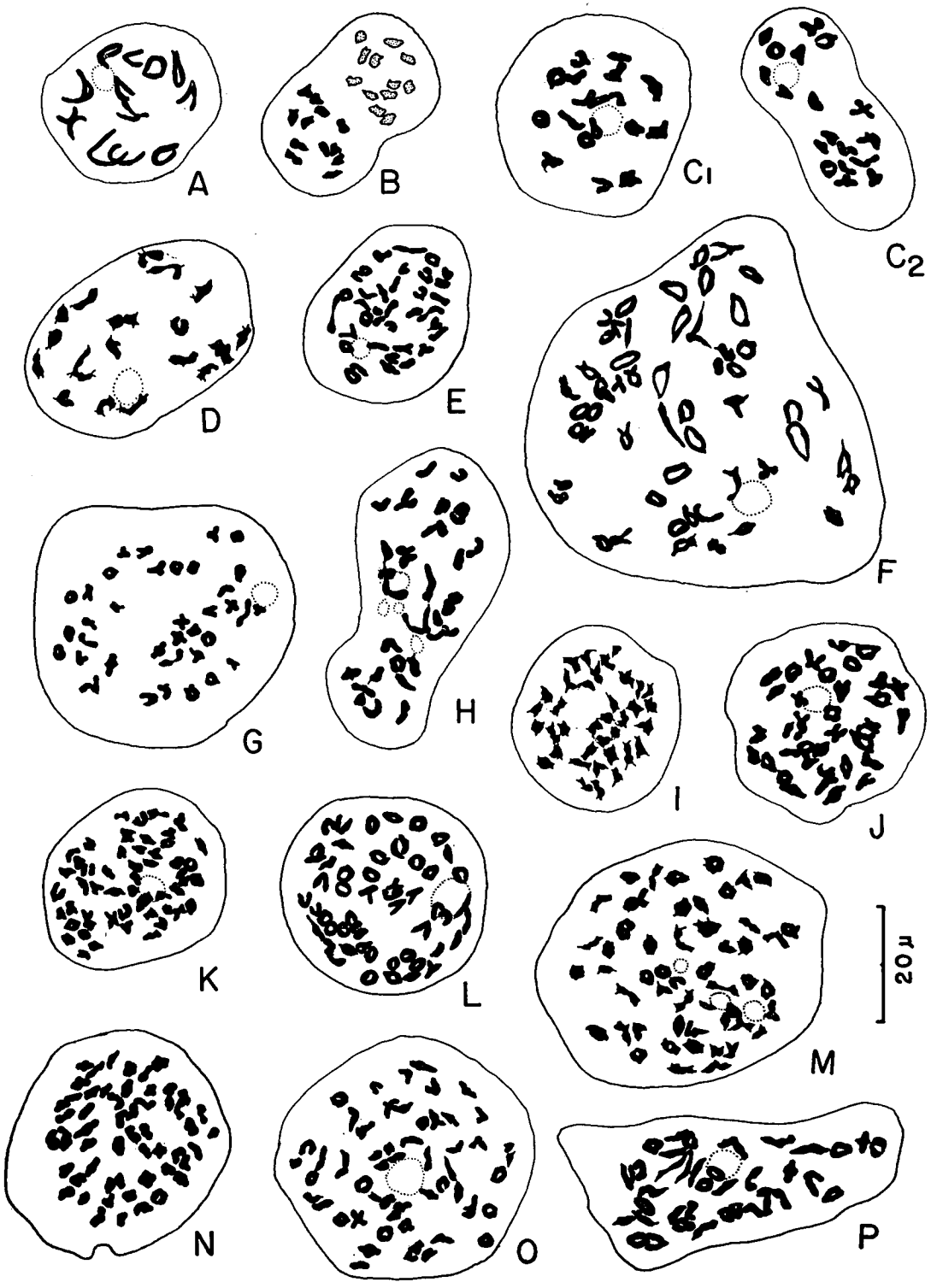

Fig. 1. Camera lucida drawings of meiotic chromosome configurations of various ragweed species. For details see text and Table 1. A, B. *Ambrosia trifida* L. (n = 12).—C. *A. canescens* (Benth.) Gray (n = 18).—D. *A. cumanensis* H. B. K. (n = 18).—E. *A. psilostachya* DC. (n = 36).—F. *A. confertiflora* DC. (n = 54).—G. *Franseria camphorata* Greene (n = 36).—H-J. *A. psilostachya* DC. (n = 36).—K-O. *A. psilostachya* DC. (n = 54).—P. *A. cheiranthifolia* Gray (n = 36).

related species of *Dicoria*, for both species of *Xanthium*, sensu Löve and Dansereau (1959), and for 24 of the approximately 30 species or species aggregates of *Ambrosia* (including *Franseria*). Thus, information is available for nearly 75% of the tribe. In the following account, species with $n = 18$ will be termed "diploid."

Neither polyploidy nor aneuploidy is known in the small, relatively homogeneous genera *Dicoria*, *Hymenoclea* and *Xanthium*, all species of which have $n = 18$, so far as is known.

Three basic numbers have been recognized in *Iva* (Jackson, 1960)—$x = 16$, 17 and 18, which have been hypothesized to represent polyploid types derived from lower numbers, such as 8, 9 and 10, found in the Heliantheae. However, the question of the original chromosome number for the genus has not been answered. In view of the rather thorough sampling of Ambrosieae, with the fact that no species with $n = 8$ or $n = 9$ have been discovered, and assuming *Iva* to be monophyletic, we believe the most likely hypothesis is that the basic number of *Iva* is $n = 18$, and that genomes of $n = 16$ and $n = 17$ have been derived by aneuploid reduction. This would be in accordance with Jackson's (1960, f. 11) ideas of the evolution of the genus. If *Iva axillaris* ($n = 18$) has been derived from *I. hayesiana* ($n = 17$) as Jackson suggests, both ascending and descending changes in chromosome number have occurred in the phylogeny of *Iva*. Polyploidy has been reported in only 1 species of *Iva*, *I. dealbata*, in which $n = 36$ (Jackson, 1960). *Iva xanthifolia* has been reported as having both $n = 18$ (Jackson, 1960) and $n = 17$ (Mulligan, 1959), and, therefore, deserves further investigation.

Among the ragweeds (*Ambrosia*, including *Franseria*) the predominance of $x = 18$ is striking. Of the 24 species studied in this group, some of which appear to be polyploid complexes or aggregates, only 2 deviate from the basic pattern of $x = 18$—*A. bidentata* ($n = 17$) and *A. trifida* ($n = 12$). Both are among the most highly specialized ragweeds, and it seems very unlikely that counts for either of these species represent basically lower numbers for this genus. Both have probably been derived by aneuploid reduction, as suggested by Jones (1933, 1943) on the basis of chromosome pairing in interspecific hybrids. Both are weedy annuals, and their reduced chromosome number accords with the suggestions made by Stebbins (1950, 1958) as to the importance of a reduced rate of recombination in such plants.

Polyploid series have been reported in at least 5 ragweed species or aggregates: *Franseria chenopodiifolia—F. deltoidea, F. dumosa* agg., *Ambrosia confertiflora* agg., *A. psilostachya* and *A. peruviana*. Available counts for the first-mentioned group are few but suggest that *Franseria deltoidea* has $n = 18$, whereas the closely similar *F. chenopodiifolia* has $n = 36$.

Franseria dumosa is a small shrub of the northern Sonoran Desert which is strikingly different from other ragweed species in the organization of its inflorescence. Chromosome numbers of $n = 18$, 36 and 54 have been counted in this species, and 1 specimen has been found to have $n = 62$ or 63, which suggests the possible existence of plants with $n = 72$. Plants of *F. dumosa*, at the diploid versus the polyploid levels, appear strikingly different in the field, in morphology as well as in time of blooming and ecological preferences. It appears likely that further study will result in taxonomic subdivision of this complex.

Ambrosia confertiflora, the third group in which different levels of polyploidy have been observed, is an extremely variable complex with little information as yet available as to the possible relationship of the different ploidal levels to recognized variants.

The numbers $n = 36$, 54 and 72 have been observed in *A. psilostachya*, an herbaceous, root-propagating perennial found throughout the central United States and Mexico. Like several other widespread weedy species in this genus, it is very heteromorphic and has a confusing taxonomic history. In general, $n = 36$ predominates in populations from the northern and eastern United States where the plants are often distinguished as var. *coronopifolia* or *A. coronopifolia*. Western populations tend to have $n = 54$ and are often distinguished as true *A. psilostachya*. Although it has been suggested that the occurrence of the different ploidal levels is correlated with the 2 taxa (Wagner and Beals, 1958), recent studies (Payne, 1962) indicate that the morphological correlations are relatively weak, with most specimens being at least partially intermediate. Similarly, a specimen from Yolo County, California, with $n = 72$ is in no way distinctive from other specimens of the same area having $n = 54$. Thus, while the occurrence of different ploidal levels undoubtedly restricts outbreeding to members of the same ploidal groups, these cannot be effectively characterized so as to provide useful species or subspecies distinctions at the present time.

Ambrosia peruviana has been observed to have both $n = 18$ (Turner, Powell, and King, 1962) and $n = 36$ (present account). However, the nature of this species is very ambiguous at present, and the name, as commonly used, probably incorporates elements of 2 groups, typical *A. peruviana* and *A. cumanensis*. These may, in turn, be subspecific members of *A. psilostachya* ($n = 36$, 54, 72) and *A. artemisiifolia* ($n = 18$), respectively. As with *A. confertiflora*, above, it is impossible at present to adequately assess the cytology of this complex.

In Table 2 the various ragweed species for which counts are available are arranged to show correlations between habit, ploidal level and weediness. All of the annual species which occur abundantly in association with man as weeds of primary sites are diploids or aneuploids pre-

TABLE 2. *Species and species complexes of Ambrosia (Franseria) arranged according to plant habit and ploidal level and scored for more or less aggressive weediness*

Species (*Ambrosia-Franseria*)	Annual	Perennial (X = herb, XX = shrub)	Diploid (X) Aneuploid (XX)	Polyploid	Strongly ruderal plants
A. acanthicarpa	X		X		X
A. artemisiifolia	X		X		X
A. bidentata	X		X X(*n* = 17)		X
A. trifida	X		X X(*n* = 12)		X
A. cumanensis		X	X		X
A. canescens		X	X		X
A. grayi (*F. tomentosa*)		X	X		X
F. artemisioides		X	X		(?)
A. polystachya		X	X		(?)
A. bryantii		X X	X		
F. deltoidea		X X	X		
A. chamissonis (*bipinnatifida* etc.)		X X	X		
F. ambrosioides		X X	X		
F. ilicifolia		X X	X		
F. eriocentra		X X	X		
F. dumosa		X X	X	X	
A. peruviana		X	X	X	X
A. cheiranthifolia		X		X	X
A. psilostachya		X		X	X
A. confertiflora		X		X	X
A. pumila		X		X	X
A. hispida		X		X	
F. camphorata		X X		X	
F. chenopodiifolia		X X		X	

sumably derived from diploids. These species tend to occur predominantly in northerly portions of the genus range. Of the weedy, herbaceous perennial species, 3 are diploid, 4 are polyploid and 1, *A. peruviana*, may have both diploid and tetraploid races. However, of these perennials, only 2, *A. psilostachya* and *A. confertiflora*, are abundant ruderal weeds with relatively extensive ranges. The perennial herbaceous species occur predominantly in the southwestern United States and Mexico in prairie and arid region associations, where their perennial nature may give them competitive advantage over annuals. Of the 9 shrubby species listed in Table 2, all but 3, *F. camphorata*, *F. chenopodiifolia* and *F. dumosa*, are diploid and the *F. dumosa* aggregate includes diploid members. These shrubby ragweeds include many of the less specialized species, as judged on the basis of floral morphology (Payne, 1963) and other characteristics. Their predominantly diploid nature supports placement near the beginning of the evolutionary scheme for the genus. Both annual and perennial, herbaceous species appear to have differentiated from shrubby progenitors on the diploid level. Polyploidy has developed in the evolution of several of the perennial herb complexes and in 3 of the shrub complexes, while aneuploid reduction has taken place during the evolution of the most specialized annuals.

In summary, the immediate basic chromosome number for the Ambrosieae appears to have been $x = 18$, with aneuploid reduction proceeding independently in *Iva* to produce genomes of $n = 17$ and $n = 16$, and in *Ambrosia* to produce genomes of $n = 17$ and $n = 12$. The tribe is, therefore, postulated to have had a polyploid origin, presumably derived from non-ambrosioid composites with $n = 9$, and to have diversified from the immediate ancestral group on the polyploid level. There is no evidence at present that species with $n = 9$ that had attained the morphological characteristics of Ambrosieae ever existed. The ragweeds have proliferated chiefly in the subarid and dry subtropical regions of southwestern North America, where many of the least specialized species, as judged on the basis of floral morphology and other characters, are endemic. It appears probable, therefore, that they actually originated in or near this region which still supports a rich flora of less specialized ragweed relatives.

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PHOSPHATASE ACTIVITY AND CELLULAR DIFFERENTIATION IN PHLEUM ROOT MERISTEM[1]

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ABSTRACT

Using 9 different organic phosphate substrates as alternatives in a standardized 5′-nucleotidase histochemical test system, enzyme activity patterns were recorded for timothy grass root epidermis. At least 4 different phosphatases were distinguished on the bases of substrate specificity, reaction rate, tissue distribution, and response to inhibitors. Except with adenosine-3′-monophosphate, all activities were restricted to the 300-μ-long root tip meristem. These enzyme activities were associated with the earliest phases of differentiation of the epidermal hair and hairless cell initials. The distribution of activities was not associated with the same cell type in each part of the meristem. Little activity was found with most substrates in the undifferentiated cells of the 0–100μ zone; alternating active hairless and inactive hair cell initials predominated in the 100–200μ segment; and active hair–inactive hairless sister cells formed the principal pattern in the 200–300μ segment of the meristem. The data showed that a particular enzyme activity was associated with a specific cell type only in relation to that cell's position along the differentiation gradient of the entire tissue. But, within a meristem segment, a specific cell type might act differently from its neighbors, depending on its mitotic capacity. This complex of physiological dependence and independence of a cell type on tissue ontogeny was cited as a characteristic of the phenomenon of cellular differentiation superimposed on tissue differentiation gradients.

VARIOUS studies have shown that the epidermal meristem of the *Phleum* root is not a homogeneous cell population. Morphological heterogeneity is obvious upon simple inspection of the tissue. Mitotic rate and the probability for further mitoses vary in different ways along the meristematic gradient (Erickson, 1961), even though mitosis is the principal developmental process there. Growth inhibitors such as coumarin and

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