A QUANTITATIVE STUDY OF VARIATION IN THE BRACTS, RAYS, AND DISK FLORETS OF ASTER SHORTII HOOK., A. NOVÆ-ANGLIÆ L., A. PUNICEUS L., AND A. PRENANTHOIDES MUHL., FROM YELLOW SPRINGS, OHIO.¹

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I. INTRODUCTION.

THE work upon which this paper is based was done in the Biological Laboratory of Antioch College, during the academic year 1900-1901, under the direction of Prof. W. L. Tower.

My primary object was to study the variations of several species of *Aster* by means of the statistical methods, to determine whether the results of Ludwig ('95, '96, '98) upon *Chrysanthemum leucanthemum* L. were also true for other nearly allied forms, and to find out, if possible, how much correlation there

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is between the observed variation and the environment, or between parts of the same plant. Secondly, it was hoped that this research might show something of the applicability of these methods to taxonomic or monographic work in a genus so difficult from the systematic standpoint as *Aster*.

II. MATERIAL.

This consisted of the blooming capitula of *Aster shortii* Hook., *A. novæ-angliæ* L., *A. puniceus* L., and *A. prenanthoides* Muhl.

The capitula were cut off without any conscious selection, folded in papers, labeled, and preserved in alcohol. With the exception of those plants where series of pickings were made, the stems from which the capitula had been gathered were preserved for future reference.

All of the species of *Aster* studied are perennial, but they differ in the manner in which the annual stems are produced. In the following description of the material used in this study I shall use the term "individual" in its broader sense, including all stems which have been derived from a single seed.

Aster shortii Hook. has from one to three or four slender annual stems arising from a small perennial root. The material which forms the basis for the study of this species was obtained Sept. 26, 1900, and consisted of 226 capitula from three isolated individuals and from a group of ten stems growing near to each other. The stems of this group were probably mostly distinct individuals, though they may have been of close genetic relationship. These plants grew in the thin limestone soil at the foot of the Niagara limestone cliffs bordering the northern end of Sheldon's Glen, one-half mile southeast of Yellow Springs, Ohio.

Aster novæ-angliæ L. has a heavy mass of perennial roots, and from the base of the annual stems of one year's growth may arise a considerable number of heavy stems of the next year's growth, forming a clump. The 199 capitula used in the study of this species were collected Sept. 30, 1900, from five individuals growing in the flood plain of a tributary to the Glen

Stream, one-half mile east of Yellow Springs, and from four individuals similarly located in the valley of the Glen Stream about forty rods above the point at which it empties into the Little Miami River, one mile southeast of Yellow Springs, Ohio.

The manner of production of annual stems in *Aster puniceus* L. resembles closely that of *Aster novæ-angliæ* L. The material of *Aster puniceus* L. used in this study was collected Sept. 25, 1900. It consisted of 798 capitula from thirteen stems arising from three perennial roots growing at the margin of a bog five miles west of Yellow Springs, Ohio. These three individuals were identically located, being separated by a space of but a few yards. Environmental conditions had, therefore, no known influence in determining the differences in the heads from the three clumps.

Aster prenanthoides Muhl. differs from all of the other species studied, in the manner in which its annual stems are produced. It sends out slender rootstocks, which give rise to new stems at a little distance from the old ones, thus forming patches with the stems growing singly.

Eighty-three capitula of *Aster prenanthoides* Muhl. were collected Sept. 27, 1900, from seven stems, apparently belonging to two individuals. The remaining material of this species, making a total of 658 capitula, was all collected from a single small plot. Four successive collections were made on September 27, September 30, October 4, and October 8, 1900. All the capitula which were blooming at the time of each collection were taken, amounting respectively to 117, 143, 139, and 176 heads, and comprising all the heads produced by the selected plot during the season. The object in collecting in this way was to test, at least within narrow limits, the constancy of the variability "constants" throughout the flowering season.

The plants from which all the material of *A. prenanthoides* Muhl. was collected grew at the bottom of a small ravine near Clifton, Ohio, at the margin of a permanent stream, so that heat, light, soil, and moisture conditions were nearly constant throughout the growing period.

III. METHODS AND PRECAUTIONS.

In order that the personal equation should modify results as little as possible, all of the heads of each individual were collected, and none were discarded on the ground of abmodality. The only material rejected was such as was eaten by insects, or had been blighted to such extent as to make a correct count impossible. It is evident that by the discarding of healthy material because of its great departure from the usual condition, or, as Strong (1901, p. 295) says, the choice of "individuals which appear on inspection to be typical," the statistical method may be made to give any result for which the investigator may be looking.

There is one element of error in the choice of material which must be mentioned. In those cases in which it seemed desirable to get curves and "constants," representing the conditions in the capitula of single individuals, there was necessarily a choice of those individuals which had the largest number of blooming heads. In this respect, therefore, the determinations would represent the conditions in the more robust specimens rather than in the general population. To counteract this tendency, there was an occasional collection of material from a sufficiently large group of smaller individuals to give equally valid results. As these collections from a number of smaller individuals did not show a marked difference from those of single larger individuals, this selection has probably not greatly modified the results.

In making counts the liability of error is not so great as in the taking of measurements. However, even in counting there are sources of error, which I found it necessary to eliminate as far as possible. To free my work as far as possible from these sources of error, the capitula were carefully dissected and the parts kept separate until the count was completed. When there was the least doubt as to the correctness of the result they were recounted. Also in cases of great abmodality the results were verified by a recount.

In calculating the various constants I have used the formulæ given by Davenport ('99). All the mathematical processes

were carried out to the tenth decimal place, and wherever practicable they were checked. It is probable, therefore, that all calculations are correct to the fifth decimal place.

In plotting the variations I have used the "method of rectangles" as best representing the actual conditions found. In those cases in which material was insufficient compared with the range of variation, I have doubled the classes, but in no case have I grouped more than two classes together. In this way the essential features of the curves have remained unchanged, while the lesser irregularities have been eliminated.

It must be remarked, however, in regard to the grouping of classes, that the method should be used with much caution. By combining a sufficient number of classes every multimodal curve may be made monomodal.

It is also essential, in doubling, that a definite plan be adopted in order that the results may be comparable. The writer followed the plan of throwing together the two classes nearest the mean. As the mean is a constant, this makes the resulting double classes of the various curves strictly comparable. If I had begun at the lower limit of range instead of at the mean, the count of one more variate might have lowered the range by one, and thus have changed the combinations, with the result that the character of the curve might be much modified.

IV. RESULTS.

Aster shortii Hook. — Fig. 1 represents the frequency polygon of the bracts. The range, 28 to 49, was so great that the 226 counts were insufficient, and it was deemed best to double the classes. In this way the curve becomes monomodal, with the mode on 36–37, and the mean on 36.800884. The coefficient of variability was 10.727157.

The frequency curve of the rays (Fig. 2) shows a remarkably strong mode on 13, 38 per cent of the variates falling into that class, with the mean on 14. This strong mode on 13 suggests at once Ludwig's ('95, '96, '98) interesting results on *Chrysanthemum leucanthemum* L., etc.; but, as nowhere else in the Asters studied has there been any apparent tendency of modes

FIG. 1.

FIG. 2.

FIG. 3.

FIG. 1. — *Aster shortii* Hook. Bract curve of 226 heads. Classes doubled. Mean = $36.800884 \pm .177121$; mode = 36-37; $\sigma = 3.947688 \pm .125243$.

FIG. 2. — *Aster shortii* Hook. Ray curve of 226 heads. Mean = $14 \pm .068448$; mode = 13; $\sigma = 1.525592 \pm .048400$.

FIG. 3. — *Aster shortii* Hook. Disk curve of 226 heads. Mean = $22.053097 \pm .067885$; mode = 22; $\sigma = 1.513025 \pm .048001$.

to fall into the series 8, 13, 21, 34, etc., this condition in *Aster shortii* Hook. cannot be considered as having any special sig-

FIG. 4. — *Aster shortii* Hook. Correlation surface for 226 heads. Rays subject and bracts relative. $\rho = .549555 \pm .025157$.

FIG. 5. — *Aster shortii* Hook. Correlation surface for 226 heads. Rays subject and disk florets relative. $\rho = .446645 \pm .029861$.

nificance in this connection. The coefficient of variability for the rays was found to be 10.897091, or a little greater than that of the bracts.

The curve of the disk florets (Fig. 3) in this species shows a remarkable lack of variation in parts which, owing to their indeterminate character, might be expected to be the most variable. The mode is on 22, the mean on 22.053097, and the coefficient of variability is only 6.860830. It should be noted that in all these curves there is negative skewness,¹ though it is slight in the bracts and disk florets. The variability constants for *Aster shortii* Hook. are shown in the following table.

TABLE A. — CONSTANTS OF ASTER SHORTII HOOK.

	BRACTS.	RAYS.	DISK FLORETS.
No.	226	226	226
Mean	36.800884	14	22.053097
Mode	36-37	13	22
A. D.	3.029211	1.176991	1.115200
σ	3.947688	1.525592	1.513025
P. E. A. D.	± 2.662716	± 1.029012	± 1.020535
P. E. M.	$\pm .177121$	$\pm .068448$	$\pm .067885$
P. E. σ	$\pm .125243$	$\pm .048400$	$\pm .048001$
C. V.	10.727157	10.897091	6.860830

In Fig. 4 is represented a "correlation surface" with rays subject and bracts relative. The coefficient of correlation was found to be .549555 (P. E. $\rho = \pm .025157$). The correlation between rays and disk florets is shown in Fig. 5, in which the coefficient of correlation is .446645 (P. E. $\rho = \pm .029861$).

Aster novæ-angliæ L. — In this species the range of variation in all the parts was great, the least range, 30 to 60, occurring in the bracts.

All the frequency polygons, Figs. 6, 7, and 8, show a multimodal condition, but this may be due to too scanty material. Although no dependence can be put upon the multimodal condition of these curves, the "variability constants" will perhaps not differ widely from results which would be given

¹ The degree of skewness has not been computed for any of the polygons of distribution because the range of material was too small to make this index of any value.

by counting larger quantities of the same material. These appear in the following table.

TABLE B. — CONSTANTS OF *ASTER NOVÆ-ANGLIÆ* L.¹

	BRACTS.	RAYS.	DISK FLORETS.
No.	199	199	199
Mean	44.030150	42.874371	62.452261
Modes	33, 37, 43, 47, 57	37, 43, 47, 51	51, 60, 63, 70
A. D.	4.111310	5.048407	7.688088
σ	5.212961	6.308112	9.314270
P. E. A. D.	± 3.516142	± 4.254822	± 6.282475
P. E. M.	$\pm .249252$	$\pm .301616$	$\pm .445352$
P. E. σ	$\pm .176248$	$\pm .213267$	$\pm .314912$
C. V.	11.839527	14.710682	14.914224

There is a high degree of correlation between rays and bracts (Fig. 9), which is the more apparent because of the close agreement in the number of rays and bracts; 10.54 per cent of all the capitula had the number of rays and bracts equal. The coefficient of correlation between these was $.802388 \pm .012685$. Between rays and disk florets the correlation (Fig. 10) was much lower, the coefficient being $.594798 \pm .024859$.

Aster puniceus L. — The polygons of distribution of the bracts (Fig. 11), rays (Fig. 12), and disk florets (Fig. 13) of *Aster puniceus* L. are all multimodal; but it would not be fair to assume that this condition is a specific one, for, although the number of variates was 798, they represent only three individuals, and these individuals had an exceedingly wide range of variation and also differed widely in the values of their "constants." These facts will be best appreciated by a study of the table on the following page.

¹ The table of constants for *Aster novæ-angliæ* L. is presented because the multimodal condition of the polygons of distribution of this species may be due to too limited material. If more material shows this same condition, then all the constants except the mean and mode must be dropped from this table. The same is also true for the constants for all of the species given in this paper.

TABLE C. — CONSTANTS OF *ASTER PUNICEUS* L.

		INDIVIDUAL No. 1. 337 heads.	INDIVIDUAL No. 2. 246 heads.	INDIVIDUAL No. 3. 215 heads.	SUMMATION, Nos. 1, 2, and 3. 798 heads.
BRACTS.	Mean . . .	42.501483	45.378048	46.795348	44.546365
	Modes . . .				35, 39, 49, 46, 48
	A. D. . . .	3.965747	3.140095	2.377501	3.571510
	σ	4.760197	3.959072	3.035446	4.497254
	P. E. A. D.	± 3.210752	± 2.670394	± 2.047408	± 3.033397
	P. E. M. . .	$\pm .174901$	$\pm .170258$	$\pm .139632$	$\pm .107381$
	P. E. σ . . .	$\pm .123673$	$\pm .120390$	$\pm .098734$	$\pm .075929$
	C. V. . . .	11.200072	8.724641	6.486640	10.095669
RAYS.	Mean . . .	35.020771	36.321138	39.660465	36.671679
	Modes . . .				27, 35, 37
	A. D. . . .	3.039368	3.421607	3.175164	3.577188
	σ	3.904214	4.297721	4.018685	4.480251
	P. E. A. D.	± 2.633392	± 2.898813	± 2.710603	± 3.021929
	P. E. M. . .	$\pm .143450$	$\pm .184821$	$\pm .184861$	$\pm .106975$
	P. E. σ . . .	$\pm .101434$	$\pm .130688$	$\pm .130716$	$\pm .075642$
	C. V. . . .	11.148282	11.832838	10.132723	12.217198
DISK FLORETS.	Mean . . .	60.513353	76.609756	74.241860	69.174185
	Modes . . .				57-58, 63-64, 67-68, 73-74, 79-80
	A. D. . . .	5.805756	8.068609	5.644478	8.947764
	σ	7.338405	10.083765	7.115330	11.116989
	P. E. A. D.	± 4.949754	± 6.801500	± 4.799290	± 7.498400
	P. E. M. . .	$\pm .269630$	$\pm .433647$	$\pm .327368$	$\pm .265440$
	P. E. σ . . .	$\pm .190657$	$\pm .306628$	$\pm .231442$	$\pm .187694$
	C. V. . . .	12.126919	13.162508	9.583987	16.071008

This work on *Aster puniceus* L. shows what a wide difference may exist, even in such constants as the means, standard deviations, and coefficients of variability, in individuals growing under apparently identical conditions.

In Fig. 14 is shown the correlation surface for rays and bracts of all the heads counted. The coefficient of correlation was $.705100 \pm .009194$, while that for rays and disk (Fig. 15) was $.674928 \pm .010045$.

Aster prenanthoides Muhl. — The frequency polygons for all the heads counted in this species are shown in Figs. 16, 17, and 18. All are multimodal, but by doubling the classes in Fig. 17, which represents the variation in the rays, the curve becomes monomodal with negative skewness, the mode being on 26–27 and the mean on 28.037993.

Doubling the classes in Fig. 16 still leaves three modes in the frequency polygon of the bracts. These modes occur on

FIG. 6. — *Aster novae-angliae* L. Bract curve of 199 heads. Classes doubled. Mean = $44.030150 \pm .249252$; modes = 33, 37, 43, 47, 57; $\sigma = 5.212061 \pm .176248$.

40–41, 44–45, and 48–49. Fig. 18 shows the curve of the disk florets to have two nearly equal modes on 48–49 and 52–53.

The correlation of rays and bracts in the 658 capitula counted (Fig. 19) is expressed by the coefficient $.776834 \pm .007820$, and that of the rays and disk florets (Fig. 20) by $.770316 \pm .008042$.

TABLE D.—CONSTANTS OF *ASTER PRENANTHOIDES* MUHL.

	BRACTS.	RAVS.	DISK FLORETS.
No.	658	658	658
Mean	44.044072	28.037993	50.297872
Mode	$\begin{cases} 40-41 \\ 44-45 \\ 48-49 \end{cases}$	26-27	$\begin{cases} 48-49 \\ 52-53 \end{cases}$
A. D.	4.497002	3.373227	4.884951
σ	5.716510	4.070071	6.310315
P. E. A. D.	± 3.855786	± 2.745263	± 4.256308
P. E. M.	$\pm .150314$	$\pm .107021$	$\pm .165889$
P. E. σ	$\pm .106288$	$\pm .075675$	$\pm .117301$
C. V.	12.979068	14.516272	12.545890

Result of the Successive Collections.—The remaining figures represent the conditions found in four successive pickings made from a single group of individuals of *Aster prenanthoides* Muhl.

1. *Bracts.* Figs. 21, 22, 23, and 24 show the frequency polygons of the bracts in the successive collections. In the first collection (Fig. 21) there was a single mode on 49-50, with the mean on 47.410256 and a strong positive skewness. In the second collection (Fig. 22) the curve broke up into three modes on 40-41, 44-45, and 48-51, while the mean fell to 44.342657. In the third collection (Fig. 23) the material exhibited two modes on 44-45 and 50-51, which correspond closely with the upper two modes of the second picking, the mean having fallen to 43.834532. At the last collection the curve, given in Fig. 24, showed a strong mode on 41-42, while the upper mode, which at this time occurred on 49-50, had become much less prominent, and a small mode had appeared on 33-34. The mean had continued to fall, and in this last collection was only 41.92045.

The table on page 124 will facilitate a comparison of the bracts from the four collections.

FIG. 7. — *Aster novae-angliae* L.. Ray curve of 199 heads. Classes doubled. Mean = $42.874371 \pm .301616$; modes = 37, 43, 47, 51; $\sigma = 6.308112 \pm .213267$.

FIG. 8. — *Aster novae-angliae* L.. Disk curve of 199 heads. Classes doubled. Mean = $62.453261 \pm .445352$; modes = 51, 60, 63, 70; $\sigma = 9.314270 \pm .314912$.

TABLE E. — CONSTANTS OF BRACTS OF FOUR PICKINGS OF
ASTER PRENANTHOIDES MUHL.

	117 CAPITULA, COLLECTED SEPTEMBER 27.	143 CAPITULA, COLLECTED SEPTEMBER 30.	139 CAPITULA, COLLECTED OCTOBER 4.	176 CAPITULA, COLLECTED OCTOBER 8.
Mean	47.410256	44.342657	43.834532	41.92045
Mode	49-50	$\begin{cases} 40-41 \\ 44-45 \\ 48-51 \end{cases}$	$\begin{cases} 44-45 \\ 50-51 \end{cases}$	$\begin{cases} 33-34 \\ 41-42 \\ 49-50 \end{cases}$
A. D.	4.350646	4.256345	4.308211	3.855552
σ	5.524237	5.152370	5.275976	4.889626
P. E. A. D. . .	± 3.726098	± 3.475273	± 3.558646	± 3.298052
P. E. M. . . .	$\pm .344540$	$\pm .290617$	$\pm .301840$	$\pm .248600$
P. E. σ	$\pm .243626$	$\pm .205497$	$\pm .213433$	$\pm .175786$
C. V.	11.651989	11.619444	12.036119	11.664053

2. *Rays*. The frequency polygon for rays from the first collection (Fig. 25) shows a strong mode on 32-35 and a lesser mode on 26-27. The mean of this collection was 30.769230. In the second collection (Fig. 26) the principal mode had fallen to 30-33, filling up the sinus and forming a monomodal curve. The mean had also fallen to 28.706293. In the third collection the rays again broke up into a multimodal condition, as shown in Fig. 27. The modes of this curve are on 24-25, 28-29, and 32-33, and the mean on 28.251798. In the fourth collection the rays again exhibited a strongly monomodal condition (Fig. 28), with the mode on 26-27, while the mean had fallen to 26.335227.

3. *Disk Florets*. In Fig. 29 is shown the multimodal frequency polygon for the disk florets of the first collection, with modes on 56-57 and 60-61, and the mean on 56.427350. In the second collection (Fig. 30) modes occurred on 45-46 and 51-52, and the mean had fallen to 51.713286. In Fig. 31 is represented the variation of the disk florets of the third collection. The curve is monomodal and nearly normal, the mode occurring on 49-50 and the mean on 49.158273. The disk curve of the fourth collection (Fig. 32) is also strongly monomodal and nearly normal, but the mode has fallen to 45-46 and the mean to 45.778409.

FIG. 9. — *Aster novae-angliae* L. Correlation surface for 199 heads. Rays subject and bracts relative. $\rho = .802388 \pm .012685$.

FIG. 10. — *Aster novae-anglicae* L. Correlation surface for 109 heads. Rays subject and disk florets relative. $\rho = .594798 \pm .024859$.

FIG. 11. — *Aster puniceus* L. Bract curve of 798 heads. Mean = $44.546365 \pm .107381$;
modes = 32, 35, 39, 46, 48; $\sigma = 4.497254 \pm .075929$.

FIG. 12. — *Aster puniceus* L. Ray curve of 798 heads. Mean = $36.671679 \pm .075642$;
modes = 27, 35, 37; $\sigma = 4.480251 \pm .075642$.

FIG. 13. — *Aster puniceus* L.. Disk curve of 798 heads. Classes doubled. Mean = $69.174185 \pm .265440$; modes = 57-58, 63-64, 67-68, 73-74, 79-80; $\sigma = 11.116989 \pm .187694$.

FIG. 14. — *Aster puniceus* L. Correlation surface for 798 heads. Rays subject and bracts relative.
 $\rho = .705100 \pm .009194$.

FIG. 15. — *Aster puniceus* L. Correlation surface for 798 heads. Rays subject and disk florets relative. $\rho = .674928 \pm .010045$.

FIG. 16. — *Aster prenanthoides* Muhl. Bract curve of 658 heads. Mean = $44.044072 \pm .150314$; modes = 32, 34, 39, 41, 43, 49; $\sigma = 5.716510 \pm .106288$.

FIG. 17. — *Aster prenanthoides* Muhl. Ray curve of 658 heads. Mean = $28.037993 \pm .107021$; modes = 27, 31, 33; $\sigma = 4.070071 \pm .075675$.

FIG. 18. — *Aster prenanthoides* Muhl. Disk curve of 658 heads. Classes doubled. Mean = $50.297872 \pm .165889$; modes 48-49, 52-53: $\sigma = 6.310315 \pm .117301$.

FIG. 19. — *Aster prenanthoides* Muhl. Correlation surface for 658 heads. Rays subject and bracts relative. $\rho = .776834 \pm .007820$.

FIG. 20. — *Aster prenanthoides* Muhl. Correlation surface for 658 heads. Rays subject and disk florets relative. $\rho = .770316 \pm .008042$.

FIG. 21.

FIG. 22.

FIG. 23.

FIG. 24.

- FIG. 21. — *Aster prenanthoides* Muhl. Bract curve of 117 heads collected September 27. Classes doubled. Mean = $47.410256 \pm .344540$; mode = 49-50; $\sigma = 5.524237 \pm .243626$.
- FIG. 22. — *Aster prenanthoides* Muhl. Bract curve of 143 heads collected on September 30. Classes doubled. Mean = $44.342657 \pm .206617$; modes 40-41, 44-45, 48-51; $\sigma = 5.152370 \pm .205407$.
- FIG. 23. — *Aster prenanthoides* Muhl. Bract curve of 139 heads collected on October 4. Classes doubled. Mean = $43.834532 \pm .301840$; modes, 44-45, 50-51; $\sigma = 5.275976 \pm .213433$.
- FIG. 24. — *Aster prenanthoides* Muhl. Bract curve of 176 heads collected on October 8. Classes doubled. Mean = $41.92045 \pm .248600$; modes = 33-34, 41-42, 49-50; $\sigma = 4.886626 \pm .175786$.

FIG. 25.

FIG. 26.

FIG. 27.

FIG. 25. — *Aster prenanthoides* Muhl. Ray curve of 117 heads collected on September 27. Classes doubled. Mean = $30.769236 \pm .248547$; mode = 26-27, 32-35; $\sigma = 3.985839 \pm .175740$.

FIG. 26. — *Aster prenanthoides* Muhl. Ray curve of 143 heads collected on September 30. Classes doubled. Mean = $28.706293 \pm .201316$; mode = 30-33; $\sigma = 3.569141 \pm .142351$.

FIG. 27. — *Aster prenanthoides* Muhl. Ray curve of 139 heads collected on October 4. Classes doubled. Mean = $28.251798 \pm .200320$; modes = 24-25, 28-29, 32-33; $\sigma = 3.501476 \pm .141641$.

FIG. 28.

FIG. 29.

FIG. 30.

- FIG. 28.—*Aster prenanthoides* Muhl. Ray curve of 176 heads collected on October 8. Classes doubled. Mean = $26.335237 \pm .153066$; mode = 26-27; $\sigma = 3.010607 \pm .108234$.
 FIG. 29.—*Aster prenanthoides* Muhl. Disk curve of 117 heads collected on September 27. Classes doubled. Mean = $56.427350 \pm .248547$; modes = 56-57, 60-61; $\sigma = 3.985839 \pm .175749$.
 FIG. 30.—*Aster prenanthoides* Muhl. Disk curve of 143 heads collected on September 30. Classes doubled. Mean = $51.713286 \pm .281728$; modes = 45-46, 51-52; $\sigma = 4.994779 \pm .199211$.

FIG. 31. — *Aster prenanthoides* Muhl. Disk curve of 139 heads collected on October 4. Classes doubled. Mean = $49.158273 \pm .279452$; mode = 49-50; $\sigma = 4.884653 \pm .197602$.

FIG. 32. — *Aster prenanthoides* Muhl. Disk curve of 176 heads collected on October 8. Classes doubled. Mean = $45.778469 \pm .242280$; mode = 45-46; $\sigma = 4.777107 \pm .171318$.

FIG. 33. — *Aster prenanthoides* Muhl. Correlation surface for 117 heads collected on September 27. Rays subject and bracts relative. $\rho = .855944 \pm .012237$.

FIG. 34. — *Aster prenanthoides* Muhl. Correlation surface for 143 heads collected on September 30. Rays subject and bracts relative. $\rho = .833702 \pm .012701$.

FIG. 35. — *Aster prenanthoides* Muhl. Correlation surface for 130 heads collected on October 4. Rays subject and bracts relative. $\rho = .798642 \pm .015133$.

FIG. 36. — *Aster prenanthoides* Muhl. Correlation surface for 176 heads collected on October 8. Rays subject and bracts relative. $\rho = .803092 \pm .013443$.

FIG. 37.—*Aster prenanthoides* Muhl. Correlation surface for 117 heads collected on September 27. Rays subject and disk florets relative. $\rho = .573693 \pm .033347$.

FIG. 38.—*Aster prenanthoides* Muhl. Correlation surface for 143 heads collected on September 30. Rays subject and disk florets relative. $\rho = .358009 \pm .042145$.

FIG. 39.—*Aster prenanthoides* Muhl. Correlation surface for 130 heads collected on October 4. Rays subject and disk florets relative. $\rho = .353102 \pm .043050$.

FIG. 40.—*Aster prenanthoides* Muhl. Correlation surface for 176 heads collected on October 8. Rays subject and disk florets relative. $\rho = .545208 \pm .012157$.

TABLE F. — CONSTANTS OF RAYS OF FOUR PICKINGS OF
ASTER PRENANTHOIDES MUHL.

	117 CAPITULA, COLLECTED SEPTEMBER 27.	143 CAPITULA, COLLECTED SEPTEMBER 30.	139 CAPITULA, COLLECTED OCTOBER 4.	176 CAPITULA, COLLECTED OCTOBER 8.
Mean	30.769230	28.706293	28.251798	26.335227
Mode	$\begin{cases} 26-27 \\ 32-35 \end{cases}$	30-33	$\begin{cases} 24-25 \\ 28-29 \\ 32-33 \end{cases}$	26-27
A. D.	3.353057	2.991736	3.012680	2.452608
σ	3.985839	3.569141	3.501476	3.010607
P. E. A. D. . .	± 2.688448	± 2.407386	± 2.361745	± 2.030654
P. E. M. . . .	$\pm .248547$	$\pm .201316$	$\pm .200320$	$\pm .153066$
P. E. σ	$\pm .175749$	$\pm .142351$	$\pm .141641$	$\pm .108234$
C. V.	12.953945	12.433306	12.393818	11.431865

The variations of the disk in the four collections may be compared in the following table.

TABLE G. — CONSTANTS OF DISK FLORETS OF FOUR PICKINGS OF
ASTER PRENANTHOIDES MUHL.

	117 CAPITULA, COLLECTED SEPTEMBER 27.	143 CAPITULA, COLLECTED SEPTEMBER 30.	139 CAPITULA, COLLECTED OCTOBER 4.	176 CAPITULA, COLLECTED OCTOBER 8.
Mean	56.427350	51.713286	49.158273	45.778409
Mode	$\begin{cases} 56-57 \\ 60-61 \end{cases}$	$\begin{cases} 45-46 \\ 51-52 \end{cases}$	49-50	45-46
A. D.	3.353057	3.925179	3.619481	3.750581
σ	3.985839	4.994779	4.884653	4.777197
P. E. A. D. . .	± 2.688448	± 3.368978	± 3.294698	± 3.222219
P. E. M. . . .	$\pm .248547$	$\pm .281728$	$\pm .279452$	$\pm .242280$
P. E. σ	$\pm .175749$	$\pm .199211$	$\pm .197602$	$\pm .171318$
C. V.	12.953947	9.661212	9.936585	10.435481

4. *Correlations.* The correlation surfaces for rays and bracts, in the four collections, are shown in Figs. 33, 34, 35, and 36, and for rays and disks in Figs. 37, 38, 39, and 40. The coefficients of correlation are arranged for comparison in the following table.

TABLE H. — CORRELATION OF RAYS AND BRACTS AND OF RAYS AND DISK FLORETS IN FOUR PICKINGS OF *ASTER* *PRENANTHOIDES* MUHL.

		117 CAPITULA, COLLECTED SEPTEMBER 27.	143 CAPITULA, COLLECTED SEPTEMBER 30.	139 CAPITULA, COLLECTED OCTOBER 4.	176 CAPITULA, COLLECTED OCTOBER 8.
Rays and Bracts	ρ P. E. ρ	.855944 $\pm .012237$	.833702 $\pm .012701$	.798642 $\pm .015133$	.803092 $\pm .013443$
Rays and Disk	ρ P. E. ρ	.573693 $\pm .033347$	.358909 $\pm .042145$	.353102 $\pm .043050$	.545208 $\pm .012157$

Inspection of this table shows that the highest degree of correlation between the parts was found at the beginning of the flowering season, and that there was a constant fall for both bracts and disk florets until near the end of the season, when the coefficient of correlation again slightly increased. The increase in the coefficient of correlation between rays and bracts in the last collection was less than the "probable error" of the determination, but that between the rays and disk florets had increased until its value was only .0284 less than in the first collection.

V. DISCUSSION OF RESULTS.

The species which have been chosen for this study are quite distinct, and although *Aster puniceus* L. and *Aster prenanthoides* Muhl. belong to the same division of the genus, *Aster novæ-angliæ* L. is more distant from these, and *Aster shortii* Hook. belongs to a division which is separated in a marked degree from the others. Considering this wide separation, it is rather remarkable that there should be so close an agreement in the number of bracts in the four species. The lower limit of range varies from 28 to 30, the upper limit from 49 to 64, and the means from 36.8 to 44.5. With the bracts so nearly constant, there is a range in the mean number of rays from 14 in *A. shortii* Hook. to 42.8 in *A. novæ-angliæ* L., and yet the degree of correlation between rays and bracts is high in all

the species studied, the coefficient of correlation between them ranging from .549 + to .802 +.

The fact that the correlation between bracts and rays was found to be greater in every case than that between rays and disk florets gave rise to the question, What is the relation existing between bracts and rays? After a careful study of the position of the rays with reference to the bracts, it seems that the rays are axillary to the bracts, and that typically a nearly constant proportion of the bracts in the capitula of a species produce rays in their axils, the rest remaining empty. The material studied showed the mean number of empty bracts in each head to be as follows: *A. shortii* Hook. 22.8, *A. prenanthoides* Muhl. 16, *A. puniceus* L. 7.9, and *A. novæ-angliæ* L. 1.2.

The number of species here studied is too small to permit the derivation of laws covering so large a genus as *Aster*, but in these four species the degree of imbrication of the involucre bracts was apparently in direct proportion to the number of empty bracts. In *A. shortii* Hook., which has so many empty bracts, the scars left by their removal occupies the convex surface of an inverted cone, the base of which served as the receptacle for the comparatively small number of florets; while in *A. novæ-angliæ* L., where almost every bract has its ray, the scars formed a narrow ring about the broad receptacle. In the former there was considerable difference in form and size between the minute outer bracts and the inner ray-bearing bracts, while in the latter all the bracts were very much alike in size and form. In a number of capitula of *A. novæ-angliæ* L. there were found more rays than bracts. Some of the more marked cases of this kind were examined and the rays distinctly seen to form a scattering second row within the full outer row which is typical of *Aster*; in other words, some of the disk florets developed ligulate corollas.

The suggestion of several writers that statistical methods will prove valuable in taxonomic work is not sustained by the results set forth in this paper. It is obviously impossible to describe a species by means of the variability constants in such manner as to allow the classification of individuals which

possess but single variates of the kind used in determining those constants.

The above-stated results in *A. puniceus* L. make obvious the same truth in regard to species such as those of Compositæ, in which the individual may have a sufficient number of variates to give a good frequency polygon and constants with small "probable errors." The wide differences between the three individuals of *A. puniceus* L. show that the variability "constants" for individuals are only in a measure less variable than the characters upon which they depend.

The study of the successive collections shows another phase of the subject of variability which would materially affect the value of statistical methods in taxonomic questions relative to the Compositæ. In these successive collections there was a continuous decline in the numbers of bracts, rays, and disk florets, and a continuous change in the position of means and modes. These results could have been in no way dependent upon unnatural conditions induced by the clipping of the heads, since even the last to bloom were well-developed buds at the time the first collection was made; and had there been a change brought about in this way, it must have been in the opposite direction, since it is a well-known fact that the removal of the earlier flowers gives increased vigor to later ones.

This continuous change of means and modes during the blooming season is suggested as a possible explanation of Lucas's ('98) results upon *Chrysanthemum leucanthemum* L., other than that of difference of locality. He found that there was a marked difference between the results obtained from material collected at Yarmouth and Grand Pic, Nova Scotia, and that collected later at Milton and Cambridge, Mass. The earlier material from Nova Scotia showed the mean on 24.389 and the principal mode on 22, while the later collection from Massachusetts had the mean on 21.61 and the mode on 21.

Ludwig ('00), in commenting on these results, attributes their deviation from his own observations to the scantiness of Lucas's material, while Lucas implies, though he does not say it definitely, that the difference is a local one. In the light of my observations on *A. prenanthoides* Muhl. it seems a fair

question whether the difference may not have been in part due to the difference in the time at which the collections were made.¹

Although the material of *A. prenanthoides* Muhl., upon which this study of successive collections is based, is even less than that used by Lucas, the constancy of the fall in numbers of all the parts can leave little doubt as to the essential correctness of my results. As a few days makes a marked difference in the condition of these variable characters, different seasons may likewise be found to give different results upon material collected from the same individuals.

As the capitula which terminate the axes in the Asters are the first to bloom, my observations on the decline in the number of parts in the heads of *A. prenanthoides* Muhl. bear a close relation to those of Burkill ('95) on *Caltha palustris* L., *Ranunculus arvensis* L., *R. bulbosus* L., *R. Ficaria*, and *Thalictrum flavum*, where he arrives at the conclusion that the "position of the flower on the axis affects the sexual organs, if they vary."²

Ludwig ('00) remarks concerning this, that "weil die Zahl der Carpelle, ebenso wie die der anderen Blüthentheile und der Blütenzahlen in der Inflorescenz von der Stellung an der Axe abhängig ist, wird man Mischcurven erhalten, wenn man die Zählungen auf sämtliche Organe der einzelnen Pflanze, nicht auf einzelne gleichwerthige Organe der verschiedenen Pflanzen

¹ Since this was written, W. L. Tower has investigated *Chrysanthemum leucanthemum* L. with reference to this point, and found that there is a continuous decrease in the values of mean and modes from the beginning to the end of the flowering season. His results will appear in *Biometrika*, vol. 1, no. 2.

² In his studies on the plants named, and others in which the number of stamens and carpels vary, he finds that "the earlier formed flowers on the plant carry more stamens or more carpels, or perhaps more of both organs, than those formed later in the season," and that "flowers holding any position of advantage on an inflorescence, *i.e.*, terminal on a cyme, or at the base of a raceme, even if not maturing earliest, carry more stamens or carpels or more of both, than in the other flowers of the same inflorescence."

Finally, he finds that in forms such as *Stellaria media*, and *Ranunculus ficaria*, which have a long flowering season, there is a noticeable decrease in the number of stamens and carpels during the flowering season, regardless of their location on the inflorescence,—a result which is closely paralleled by my work on *Aster prenanthoides* Muhl.

ausdehnt, und zur Bestimmung der constanten Mischcurve der Art ist eine sehr grosse Anzahl von Zählungen nöthig."

I agree with Ludwig that a large number of counts is necessary for the determination of the constants in material of this kind; but how great must it be? It is to be noted that, in his tables representing the variation in number of achenes in the heads of *Ranunculus acris* L., he gives the results of two sets of observations, each consisting of counts of 1000 heads. The maxima of the two multimodal curves formed, alternate with each other, and their summation gives but few maxima where they ought (?) to be, — the material is insufficient; yet he makes virtue of the fact that the summation of Lucas's data, only 831 counts, presents maxima upon the series of Fibonacci.

This series of Fibonacci, which is of recognized importance in the phyllotaxy of flowering plants, should be accepted with caution as the key to all variation among plants. The members of the series, along with Ludwig's "Unterzahlen," which are made up from the numbers of the Fibonacci series by multiplication or addition, — *e.g.*, $10 = (2 \times 5)$, $29 = (8 + 21)$, etc., — include so large a proportion of all the smaller numbers that many modes must fall on or near one of them, even if there be no fundamental relation existing between this complex series and the number of floral parts or other organs under consideration. To account for modes which do not fall on any of these, Ludwig creates the "Scheingipfel," which is formed by the overlapping of curves having their modes on adjacent numbers of the Fibonacci-Ludwig complex. Thus, if the maximum falls upon 9, it is a "Scheingipfel" formed by the union of curves having maxima upon 8 and 10; if it fall upon 11, it is made up of curves having maxima upon 10 and 13, etc. It is evident that such a scheme will furnish an explanation of almost any condition which might arise.

In conclusion, it needs to be said that there remains much to be done in determining the many causes of variation. The quantitative study of variation shows only the existing condition of the material studied. It deals only with results, and if there has been no intentional selection of material, it indicates nothing as to the causes which have brought about those results.

While deprecating the selection of material on false bases, I take it that intelligent selection of material existing under known conditions is more certain to give valuable results than at-random selection, which, while sure to select, ignores the conditions under which the selection is made.

Until we know the causes of variation and how great degree of variation may be produced by how slight causes, all generalizations based upon limited observations should be accepted with caution. Granting that observers have no preconceived notions as to what they ought to find, the conditions found by each investigator are true of the material upon which he worked, but how true his general conclusions are, further investigation alone can tell.

If every valley and hillside is to have its own place-mode and every day and every season is to bring forth a changed condition in the variable characters of its living forms, only a universal collection of material covering a long period of years can give us true constants which may be verified by a repetition of the process.

VI. SUMMARY.

Quantitative studies were made upon the bracts, rays, and disk florets of four species of *Aster* growing at Yellow Springs, Ohio.

A close correlation was found between bracts and rays, and attributed to the fact that the rays are axillary to the bracts.

The degree of imbrication of the bracts was observed to bear a relation to the number of empty bracts.

Curves and "constants" were determined for the material of the four species studied. "Constants" determined for several individuals of *A. puniceus* L. growing in identical surroundings indicated how great variations may exist in the variability "constants" of individuals.

Studies upon successive collections from a single group of specimens of *A. prenanthoides* Muhl. showed that the number of bracts, rays, and disk florets all decrease continuously from the beginning to the end of the flowering season, and that the

character of the curves and the position of their means and modes likewise change continuously.

I wish to express my thanks to Prof. W. L. Tower for his kindly interest and helpful suggestion during the prosecution of these studies, and also for the revision of the manuscript.

YELLOW SPRINGS, OHIO.

June 25, 1901.

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